Identity of *Hypostomus plecostomus* (Linnaeus, 1758), with an overview of *Hypostomus* species from the Guianas (Teleostei: Siluriformes: Loricariidae)

by

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ABSTRACT. - Twenty-one nominal species of *Hypostomus* are recorded in fresh and brackish waters of the Guianas from the Oyapock to the Essequibo Rivers. One of those, *Hypostomus plecostomus*, was the first described representative of the genus. However this name was often erroneously applied to numerous other species. The identity of *H. plecostomus* was here investigated based on a dual approach allying classical morphometric and allozyme analyses of several populations representing respectively 15 and five of the Guianese species. Morphometric analyses revealed four morphological groups among the different populations, namely the *H. plecostomus*, *H. watwata*, *H. gymnorhynchus*, and Boeseman's species groups. The discriminant model used for *a posteriori* assignment of the Linnean type specimens of *H. plecostomus* to an extant species showed that the type series was heterogenous and comprised two species: *H. plecostomus* and *H. watwata*. A lectotype was designated to stabilize the taxonomy of *H. plecostomus* and its junior synonyms *H. guacari* and *H. flava*. *Hypostomus plecostomus* was also recognized based on fixed allelic differences with other *Hypostomus* species analysed. Its expected heterozygosity (0.091) was relatively high, with little differentiation between populations. Both analyses highlighted that *H. plecostomus* was a widespread species mostly distributed in the lower part of Guianese rivers. A complementary description of the species was provided. Our analysis of the *Hypostomus* material from the Oyapock to the Essequibo River basins revealed 15 potentially valid species, and new synonymies for *H. plecostomus*, *H. gymnorhynchus* and *H. corantijni* were proposed. The current distribution of the recognized species was specified.

RÉSUMÉ. - Identité de *Hypostomus plecostomus* (Linnaeus, 1758), avec une revue des espèces d'*Hypostomus* des Guyanes (Teleostei: Siluriformes: Loricariidae).

Vingt-et-une espèces nominales d'*Hypostomus* sont connues des eaux douces et saumâtres des Guyanes du fleuve Oyapock à l'Essequibo. L'une d'elles, *Hypostomus plecostomus*, fût le premier représentant du genre à être décrit, cependant ce nom est souvent appliqué à de nombreuses autres espèces. L'identité de *H. plecostomus* a été ici examinée par une double approche alliant morphométrie classique et analyse des allozymes pour différentes populations représentant, respectivement, 15 et 5 des espèces guyanaises. Les analyses morphométriques ont révélé que les différentes populations formaient quatre groupes morphologiques distincts, nommés groupes *H. plecostomus*, *H. watwata*, *H. gymnorhynchus*, et "Boeseman". Le modèle discriminant utilisé pour l'assignation à posteriori des spécimens type linnéens de *H. plecostomus* à une espèce actuelle a montré que la série type était hétérogène et comprenait deux espèces : *H. plecostomus* et *H. watwata*. Un lectotype a été désigné afin de stabiliser la taxonomie de *H. plecostomus* et de ses synonymes juniors *H. guacari* et *H. flava*. *Hypostomus plecostomus* a été également caractérisé sur la base de différences alléliques fixes au regard des autres espèces d'*Hypostomus* analysées. Le taux d'hétérozygotie attendue (0,091) s'est révélé relativement haut, avec peu de différence entre populations. Les deux analyses ont révélé que *H. plecostomus* était une espèce largement distribuée dans la partie basse des rivières guyanaises. Une description complémentaire de l'espèce est fournie. Notre analyse du matériel d'*Hypostomus* des bassins de l'Oyapock à l'Essequibo a révélé 15 espèces potentiellement valides et de nouvelles synonymies sont proposées chez *H. plecostomus*, *H. gymnorhynchus* et *H. corantijni*. La distribution actuelle des espèces reconnues a été précisée.

Key words. - Catfish - Morphometry - Allozyme electrophoresis - Genetic variation - Neotropics - French Guiana - Suriname - Guyana.

Use of the name *Hypostomus plecostomus*

The name *Hypostomus plecostomus* (Linnaeus, 1758) has often been applied to any of several distinct species of South and Central American mailed catfishes included in the genus *Hypostomus* Lacepède, 1803 and even to other Hypostominae genera. It occurs inappropriately in reports (e.g., Benson *et al*., 2004; Anderson *et al*., 2005), check-lists of invasive species (e.g., McCann *et al*., 1996), official documents (e.g., Gutiérrez and Reaser, 2005), and within anatomical (e.g., Fernandes and Perna, 1995; Mattias *et al*., 1996), parasitological (e.g., Kritsky and Boeger, 1991), physiological and ecological studies (Mazzoni *et al*., 2010) and recently in a

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study of the trophic ecology of invasive suckermouth catfish in Texas (Pound *et al*., 2011). The main reasons for the extensive use of this name are that *Hypostomus plecostomus* was not only described since the beginning of the Linnean system, but also *Hypostomus* is widely distributed, and one of the most species-rich genera of Loricariidae, with 127 species (Ferraris, 2007; Jerep *et al*., 2007; Birindelli *et al*., 2007; Zawadzki *et al*., 2008a, 2008b, 2010; Hollanda Carvalho *et al*., 2010) including numerous species with unclear taxonomic status.

Historical account

This species first appeared in a pre-Linnean description of *Acipenser indicus* by Linnaeus (1754). Four years later, Linnaeus (1758) established the new taxon *Acipenser plecostomus*, making references to his earlier publication and to the also pre-Linnean description of a species identified as *Plecostomus* by Gronovius (1754), specifying its habitat as "Surinami". The genus *Hypostomus* was later described by Lacepède (1803), including a single species described as *Hypostomus guacari* based on numerous literature sources, including the account of *Acipenser plecostomus* Linnaeus, 1758. *Hypostomus guacari* Lacepède, 1803, is therefore type species of *Hypostomus* by monotypy. One year later, Shaw (1804) described *Loricaria flava*, again based on different works including that of Linnaeus. Type specimens of *Hypostomus plecostomus* are thus also type specimens of *H. guacari* and of *L. flava* (Ferraris, 2007), two species since long placed in the synonymy of *H. plecostomus*. The nomenclatural imbroglio involving that fish continued with Kner (1854), Bleeker (1862-1863, 1864), and later authors.

During the 19th and the first half of the 20th century, while ichthyologists like Steindachner (1877a, 1877b, 1878, 1881), Regan (1904, 1908a, 1908b, 1912) and Fowler (e.g., 1915, 1941, 1943) described numerous new species of *Hypostomus* from the Neotropical freshwaters, Fowler (1954), van der Stigchel (1946), and other authors synonymised numerous species with *H. plecostomus*. Unfortunately, the latter works were widely regarded as authoritative references, so that *H. plecostomus* was mentioned from numerous Neotropical rivers and places, as in Fowler (1954: 191-192): "Amazônia, Rio Tocantins, Rio Tapajós, Rio Paranaiba, São Paulo, Paraná, Rio Grande do Sul, Paraguay, Bolívia, Peru, Colombia, Venezuela, Guianas, Trinidad". As a consequence, the species is also listed in large fish fauna's revisions, like that of Panama by Meek and Hildebrand (1916), and of Venezuela by Schultz (1944). Eigenmann (1922) himself described a new subspecies, *Plecostomus plecostomus panamensis*. None of these works was based on the examination of type specimens of *Hypostomus plecostomus*, which were regarded as lost (see Boeseman, 1968: 11).

Search for the identity of *Hypostomus plecostomus*

The first serious attempt to clear up the problematic identity of *Hypostomus plecostomus* was that of Boeseman (1968), who confirmed the validity of *Hypostomus* Lacepède, 1803 and of *Hypostomus plecostomus* (Linnaeus, 1758). He also designated a neotype in order to fix the species and revise its identity. However, this neotype designation was done despite being aware of the possible existence of Linnean syntypes, which became effectively confirmed by Fernholm and Wheeler (1983) in an annotated catalogue of the Linnean fish specimens deposited in the Naturhistoriska Riksmuseet in Stockholm (NRM). These authors found three putative syntypes in a jar (NRM 32) and, based on their examination in regard to Linnaeus works, they argued that at least the smallest was to consider as a type. Examination of this material was thus a prerequisite to the present study. We had recently the opportunity to go to Stockholm for examination of the external morphology and photographs of putative Linnaeus' type specimens of loricariids, including *H. plecostomus*.

Allozyme analysis as molecular tool for inferring species limits

External morphology, that is susceptible to environmental influences, may distinguish morphotypes within a single species. Conversely, external morphology is often hardly able to discriminate sibling species. Identification of species boundaries in such cases has benefitted from molecular techniques (Hillis *et al*., 1996), and more particularly, numerous species of fish and other organisms have been confirmed using allozyme electrophoresis (Larson, 1989; Lessios *et al*., 1995; Emberton *et al*., 1995; Allibone, 1996). Analysis of allozymes (Prakash *et al*., 1969), or the different forms of an enzyme encoded at a same locus, allows the identification of alleles, the calculation of allelic and genotypic frequencies of populations, and the estimation of genetic flow between populations. In case of sympatry, a single fixed allozymic difference between populations is sufficient to both recognize and characterize two coexisting species, as it shows that interbreeding is not occurring (Richardson *et al*., 1986). In case of allopatry, the extent of allozymic divergence between populations has to be assessed taking into account their geographical variation, a conservative approach being to consider only fixed allozymic differences, rather than measurements based on allele frequency differences, and to ally other data to determine specific status (Richardson *et al*., 1986; Thorpe and Solé-Cava, 1994). Systematics of several loricariid taxa including *Hypostomus* has been investigated with this tool leading to the discrimination of congeneric species (Zawadzki *et al*., 1999, 2000, 2001; de Paiva *et al*., 2005; Renesto *et al*., 2007), to the discovery of cryptic ones (Fisch-Muller *et al*., 2001), and to the inference of phylo-

genetic relationships (Zawadzki *et al.*, 2005; Renesto *et al.*, 2007).

Objectives of present work

In the present work, we integrated genetics with classical morphometry in order to redefine the enigmatic *Hypostomus plecostomus*. The three rediscovered syntypes were compared to hundreds of *Hypostomus* specimens from the Guianas representing 15 nominal species by means of classical multivariate morphometric analyses. Most of this material was collected by the authors and collaborators during the past 15 years (see Le Bail *et al.*, 2012; Mol *et al.*, 2012). A significant part of the specimens was specifically sampled for diverse genetic studies, including an allozyme analysis that was conducted at the MHNG. The taxonomy of *H. plecostomus* is here accordingly redefined and a complementary description provided. The taxonomic status of several of the 21 nominal Guianese species of *Hypostomus* occurring from the Oyapock to the Essequibo Rivers is also revised to establish a list of presumably valid species of the region.

MATERIAL AND METHODS

Morphometry

Specimens examined in this work represent 15 nominal species from the Guianas, and are detailed in the list of Material examined. Institutional acronyms follow Fricke and Eschmeyer (2010). Specimens were measured with a digital calliper to the nearest 0.01 mm following Boeseman (1968). Counts followed Weber (1985). Replacement teeth were examined following Muller and Weber (1992).

Morphometric analyses were based on 15 continuous morphometric variables (listed in table I, with abbreviations in squared brackets) of 287 examined specimens, with the addition of 236 specimens examined by Boeseman (1968: tables 1-20), leading to a total of 523 specimens representing 43 samples of populations for 15 nominal species. Specimens smaller than 30 mm were excluded from the analyses to minimize the bias introduced by allometric growth, and because morphometric data are highly correlated between them, missing data were estimated using the least squares method with the standard length (SL) used as explanatory variable. To estimate the absence of significant differences between measurements provided by Boeseman and ours, a Wilcoxon matched pairs signed rank test was performed on all common measurements recorded from the holotype of *H. gymnorhynchus*. In order to highlight the morphological structure of the species and populations under study, and to construct the model used for the assignment of the Linnean types to an extent species, the data were submitted to multivariate analyses. To prevent artificial groupings, the different populations collected in different basins for a given species were considered independently. Prior to the analyses, all measurements were standardized by the SL and log transformed to control for size effect. The final table included thus 523 rows representing 43 populations and species of *Hypostomus*, and 14 columns. This table was then submitted to a principal components analysis (PCA) using the correlation matrix to reveal its structuring. The PCA was secondarily submitted to a linear discriminant analysis (DA) using the 43 populations and species as grouping factor. Prior to the DA, a non-parametric version of the Pillai test was conducted using 9,999 random permutations to test against the null hypothesis of equality of means between groups. The constructed discriminant functions were subsequently used for the assignment of supplementary rows (herein NRM type specimens). The robustness of the model was estimated by cross validation to evaluate the rate of wrong assignments of individuals to their respective class. Multivariate analyses were performed with the MASS 7.3-7 (Venables and Ripley, 2002), ade4 1.4-16 (Dray and Dufour, 2007) and ade4TkGUI 0.2-5 (Thioulouse and Dray, 2007) packages in R 2.12.1 (R Development Core Team, 2009). Populations and species' scores onto discriminant axes were secondarily converted into a distance matrix. This transformation allowed a hierarchical classification of the different populations and species of *Hypostomus* represented in a dendrogram. Euclidian distances were measured between the centres of gravity of each class of individuals and analysed using the Weighted Pair-Group Method using Arithmetic means (WPGMA) algorithm (McQuitty, 1966). The WPGMA was favoured since the size of the different clusters was suspected to be greatly uneven due to the numerous species described by Boeseman (1968, 1969). Robustness of the results was estimated using a multiscale bootstrap resampling procedure (Shimodaira, 2002, 2004). For each cluster in the hierarchical clustering, *p*-values were calculated to indicate how strong the cluster was supported by the data. Two types of *p*-values were computed for each node: Approximately Unbiased (AU) (Shimodaira, 2002; 2004) and Bootstrap Probability (BP) (Efron, 1979; Felsenstein, 1985). Cluster analysis and multiscale bootstraps were performed using 1,000 pseudoreplicates with the pvclust 1.2-1 package (Suzuki and Shimodaira, 2004) in R.

Allozyme electrophoresis

A total of 188 specimens (identified by the mention of individual field numbers in the list of Material examined) representing 18 samples of populations originally attributed to five *Hypostomus* species (*H. plecostomus*, *H. ventromaculatus*, *H. watwata*, *H. gymnorhynchus*, and *H. tapanahoniensis*) were analysed for allozymes. Two additional representatives of *Hypostomus watwata* (one from Mahury and a second from Kourou Rivers) and a unique sample of *H. corantijni* were also stained for allozymes. These samples were not

Table I. - Descriptive morphometrics and meristics for 21 samples of *Hypostomus* populations from French Guiana and Suriname, and of type material of *H. plecostomus* and *H. watwata*, with their abbreviations in brackets. Asterisks indicate data from Boeseman (1868). Abbreviations for morphometric variables used in morphometric analyses are provided in square brackets. N: number of specimens.

Species	*Hypostomus plecostomus*							
Former identification	*H.* cf. *ventromaculatus*							
Locality & acronym of population	Oyapock (VOya)		Kaw (VKaw)		Mahury (VCay)		Kourou (VKou)	
N	28		16		4		16	
	range	mean ± sd	range	mean ± sd	range	mean ± sd	range	mean ± sd
Morphometry								
Standard length (SL)	165.40 - 249.80	209.31 ± 21.08	145.50 - 248.30	213.07 ± 25.65	158.40 - 192.80	176.75 ± 14.71	132.20 - 212.40	177.58 ± 20.14
Percents of SL:								
Predorsal length [Predors_l]	37.45 - 40.76	39.07 ± 0.87	37.54 - 42.51	40.13 ± 1.27	38.07 - 39.76	38.97 ± 0.86	37.77 - 40.02	38.68 ± 0.75
Head length [Head_l]	30.73 - 33.31	31.90 ± 0.76	31.35 - 34.48	33.01 ± 1.06	30.76 - 32.51	31.57 ± 0.74	30.34 - 33.21	31.51 ± 0.86
Dorsal-fin spine [Dspine_l]	28.58 - 36.93	34.11 ± 2.07	29.19 - 37.18	33.52 ± 2.51	31.64 - 37.18	34.03 ± 2.33	28.94 - 35.93	32.29 ± 2.00
Interdorsal length [Interdor_l]	15.24 - 20.81	18.23 ± 1.23	15.78 - 21.13	18.25 ± 1.52	17.65 - 18.83	18.23 ± 0.59	16.27 - 19.78	18.01 ± 1.07
Caudal-peduncule length [Peduncl_l]	30.07 - 34.89	32.81 ± 1.11	29.59 - 34.93	31.70 ± 1.58	31.75 - 33.04	32.44 ± 0.58	24.88 - 36.76	31.99 ± 2.42
Caudal-peduncule depth [Peduncl_d]	9.78 - 11.16	10.34 ± 0.37	9.88 - 11.30	10.40 ± 0.42	9.40 - 10.13	9.84 ± 0.34	9.39 - 10.55	10.14 ± 0.30
Percent of head length (HL):								
Cleithral width [Cleitr_w]	87.07 - 104.40	99.50 ± 3.21	98.74 - 105.43	101.96 ± 2.09	93.20 - 96.46	94.83 ± 1.34	90.89 - 101.99	96.31 ± 2.93
Head depth [Depth_head]	57.32 - 68.64	62.46 ± 3.17	55.65 - 75.97	68.02 ± 5.45	59.38 - 61.84	61.08 ± 1.14	58.18 - 68.43	63.00 ± 2.85
Snout length [Snouth_l]	57.40 - 61.56	59.65 ± 0.93	57.06 - 60.35	59.30 ± 0.80	56.70 - 58.68	57.57 ± 0.82	56.54 - 60.46	58.97 ± 0.93
Orbital diameter [Orbit_d]	14.16 - 16.67	15.23 ± 0.67	14.23 - 16.36	15.22 ± 0.70	16.58 - 17.71	17.23 ± 0.49	15.77 - 18.68	17.08 ± 0.84
Interorbital length [Interorb_l]	40.30 - 44.56	42.37 ± 1.10	40.06 - 44.42	42.64 ± 1.44	41.71 - 43.51	42.19 ± 0.88	40.15 - 43.87	42.55 ± 1.00
Other percentages:								
Caudal-peduncule depth % of interdorsal length	49.54 - 70.13	57.03 ± 5.05	49.45 - 71.58	57.46 ± 6.29	50.44 - 57.38	54.09 ± 3.48	47.46 - 64.04	56.70 ± 4.09
Caudal-peduncule depth % of peduncule length	28.04 - 35.42	31.56 ± 1.67	28.89 - 37.73	32.93 ± 2.64	29.60 - 30.83	30.34 ± 0.54	28.92 - 35.45	31.87 ± 1.60
Dentary length % of interorbital length	28.57 - 37.33	31.46 ± 2.07	25.82 - 33.02	29.36 ± 2.04	28.87 - 36.05	31.09 ± 3.35	23.89 - 37.80	29.21 ± 3.55
Counts								
Number of premaxillary teeth (L)	19 - 39	32 ± 4	24 - 36	31 ± 3	29 - 45	36 ± 7	23 - 40	32 ± 5
Number of premaxillary teeth (R)	22 - 42	32 ± 4	24 - 39	31 ± 4	29 - 41	34 ± 5	23 - 41	31 ± 7
Number of dentary teeth (L)	19 - 39	30 ± 5	25 - 38	31 ± 4	28 - 41	34 ± 5	22 - 38	31 ± 5
Number of dentary teeth (R)	22 - 41	30 ± 5	27 - 40	30 ± 4	29 - 39	33 ± 4	21 - 41	32 ± 7
Number of plates in the lateral series (L)	26 - 27	27 ± 0	26 - 28	27 ± 0	27 - 27	27 ± 0	26 - 27	27 ± 0
Number of plates in the lateral series (R)	26 27	27 ± 0	26 - 28	27 ± 0	27 - 27	27 ± 0	26 - 27	27 ± 0
Number of predorsal rows of plates	2 - 3	3 ± 1	3 - 3	3 ± 0	3 - 3	3 ± 0	3 - 3	3 ± 0
Number of dorsal plates	8 9	9 ± 0	8 - 9	9 ± 1	8 - 9	9 ± 1	7 - 9	8 ± 1
Number of plates between dorsal and adipose fins	6 - 8	7 ± 1	6 - 8	7 ± 1	6 - 7	7 ± 1	6 - 8	7 ± 1
Number of plates between adipose and caudal fins	7 - 8	8 ± 0	7 - 9	8 ± 1	7 - 8	8 ± 1	7 - 9	8 ± 0
Number of plates between anal and caudal fins	14 - 15	14 ± 0	13 - 15	14 ± 1	14 - 15	14 ± 1	13 - 15	14 ± 0

Table I. - Continued.

Species	*Hypostomus plecostomus*								
Former identification	*H. ventromaculatus*								
Locality & acronym of population	Mana + Maroni (VMar)		Maroni (VMarB)*		Suriname. Paramaribo (VSur)		Suriname (VCom) + (VMak)*		
N	26		3		11		13		
	range	mean ± sd	range	mean ± sd	range	mean ± sd	range	mean ± sd	holotype
Morphometry									
Standard length (SL)	119.60 - 212.40	167.40 ± 25.68	72.00 - 107.00	84.33 ± 19.66	135.20 205.00	161.73 ± 23.10	56.00 - 150.00	92.08 ± 31.61	150.00
Percents of SL:									
Predorsal length [Predors_l]	38.47 - 43.28	40.16 ± 1.09	40.37 - 42.57	41.81 ± 1.25	38.00 ± 42.90	40.56 ± 1.45	40.07 - 42.32	41.33 ± 0.76	40.07
Head length [Head_l]	31.06 - 34.62	32.69 ± 0.89	33.64 - 37.30	36.01 ± 2.05	30.39 ± 35.28	32.98 ± 1.34	32.00 - 36.79	35.18 ± 1.32	32.00
Dorsal-fin spine [Dspine_l]	28.41 - 35.70	32.47 ± 1.90	36.45 - 37.36	36.90 ± 0.65	32.54 ± 41.86	35.49 ± 3.00	32.46 - 40.62	36.42 ± 2.12	34.47
Interdorsal length [Interdor_l]	15.15 - 19.40	17.89 ± 1.02	16.62 - 17.29	17.00 ± 0.34	16.12 ± 20.67	18.04 ± 1.40	15.43 - 17.92	16.63 ± 0.69	16.53
Caudal-peduncule length [Peduncl_l]	28.34 - 33.24	31.15 ± 1.28	29.46 - 32.08	30.48 ± 1.40	27.59 ± 32.49	31.28 ± 1.48	28.08 - 29.23	28.79 ± 0.31	29.00
Caudal-peduncule depth [Peduncl_d]	10.11 - 11.52	10.79 ± 0.32	9.86 - 10.37	10.17 ± 0.27	10.18 ± 11.76	10.79 ± 0.39	9.82 - 10.77	10.28 ± 0.34	10.33
Percent of head length (HL):									
Cleithral width [Cleitr_w]	94.92 - 106.61	99.93 ± 2.79	84.64 - 93.06	87.86 ± 4.54	96.69 ±107.38	101.10 ± 3.17	83.90 - 99.38	90.25 ± 5.66	99.38
Head depth [Depth_head]	62.28 - 68.61	65.64 ± 1.88	51.31 - 56.94	54.68 ± 2.98	64.19 ± 69.85	66.62 ± 1.95	51.46 - 61.71	56.33 ± 3.46	61.67
Snout length [Snouth_l]	57.00 - 60.99	58.96 ± 1.08	53.93 - 55.56	54.97 ± 0.90	58.85 ± 61.67	60.17 ± 0.80	52.91 - 61.86	56.71 ± 2.91	60.00
Orbital diameter [Orbit_d]	14.74 - 19.31	17.04 ± 1.41	19.93 - 20.60	20.36 ± 0.38	15.88 ± 17.78	16.99 ± 0.57	17.92 - 22.33	20.34 ± 1.38	17.92
Interorbital length [Interorb_l]	39.42 - 44.97	42.05 ± 1.36	38.77 - 41.67	39.80 ± 1.62	41.44 ± 46.90	43.52 ± 1.79	37.91 - 42.37	40.71 ± 1.23	41.04
Other percentages:									
Caudal-peduncule depth % of interdorsal length	52.92 - 70.77	60.56 ± 4.20	59.35 - 60.16	59.84 ± 0.43	51.81 ± 72.94	60.26 ± 6.33	57.89 - 66.40	61.88 ± 2.56	62.50
Caudal-peduncule depth % of peduncule length	31.27 - 39.40	34.72 ± 1.94	32.03 - 34.69	33.40 ± 1.33	31.35 ± 42.63	34.62 ± 2.95	34.16 - 37.89	35.71 ± 1.17	35.63
Dentary length % of interorbital length	27.65 - 34.91	31.09 ± 2.32	- -	- -	23.20 ± 30.53	26.44 ± 2.36	- -	- -	-
Counts									
Number of premaxillary teeth (L)	23 - 42	31 ± 5	- -	- -	22 ± 28	25 ± 2	- -	- -	-
Number of premaxillary teeth (R)	22 - 45	31 ± 6	- -	- -	22 ± 29	25 ± 2	- -	- -	-
Number of dentary teeth (L)	20 - 41	30 ± 5	- -	- -	19 ± 27	23 ± 2	- -	- -	-
Number of dentary teeth (R)	24 - 41	31 ± 5	- -	- -	21 ± 29	25 ± 2	- -	- -	-
Number of plates in the lateral series (L)	27 - 28	27 ± 0	- -	- -	26 ± 27	27 ± 1	- -	- -	-
Number of plates in the lateral series (R)	27 - 28	27 ± 0	- -	- -	26 ± 27	27 ± 0	- -	- -	-
Number of predorsal rows of plates	2 - 3	3 ± 0	- -	- -	3 ± 3	3 ± 0	- -	- -	-
Number of dorsal plates	8 - 9	9 ± 0	- -	- -	8 ± 9	8 ± 0	- -	- -	-
Number of plates between dorsal and adipose fins	6 - 8	7 ± 1	- -	- -	6 ± 7	7 ± 0	- -	- -	-
Number of plates between adipose and caudal fins	7 - 8	8 ± 0	- -	- -	7 ± 8	8 ± 0	- -	- -	-
Number of plates between anal and caudal fins	13 - 15	14 ± 0	- -	- -	13 ± 15	14 ± 1	- -	- -	-

Table I. - Continued.

Species	*Hypostomus plecostomus*								
Former identification	*H. plecostomus*							*H. hemiurus*	
Locality & acronym of population	Commewijne (PMap)		Suriname. Paulus Creek (PPaK)		Saramacca (PSarB)*		(Psyn1)	Essequibo (HemE)	
N	8		17		12			4	
	range	mean ± sd	range	mean ± sd	range	mean ± sd	lectotype	range	mean ± sd
Morphometry									
Standard length (SL)	92.70 - 141.60	117.33 ± 16.57	161.80 201.90	175.39 ± 11.44	100.00 - 115.00	107.25 ± 6.09	57.80	98.25 - 141.10	116.24 ± 21.07
Percents of SL:						±			
Predorsal length [Predors_l]	39.15 - 41.99	40.47 ± 0.96	39.35 - 41.94	40.76 ± 0.85	38.14 - 42.70	40.94 ± 1.11	43.08	38.41 - 39.20	38.88 ± 0.38
Head length [Head_l]	31.00 - 34.48	33.38 ± 1.23	31.71 - 33.76	32.93 ± 0.65	33.04 - 36.20	34.87 ± 0.91	37.46	32.13 - 34.23	32.91 ± 0.95
Dorsal-fin spine [Dspine_l]	27.80 - 38.05	34.07 ± 4.43	31.20 - 37.22	35.41 ± 1.75	35.44 - 38.94	36.83 ± 1.22	-	29.88 - 33.01	30.92 ± 1.41
Interdorsal length [Interdor_l]	17.23 - 19.14	18.35 ± 0.64	16.55 - 21.16	18.93 ± 1.20	16.00 - 18.35	17.11 ± 0.85	17.13	17.99 - 18.82	18.34 ± 0.36
Caudal-peduncule length [Peduncl_l]	29.52 - 32.45	31.21 ± 1.16	29.60 - 32.60	31.15 ± 1.03	27.62 - 31.20	29.50 ± 0.94	31.49	29.66 - 30.72	30.13 ± 0.52
Caudal-peduncule depth [Peduncl_d]	9.54 - 10.77	10.36 ± 0.39	10.27 - 11.67	10.94 ± 0.36	10.27 - 10.98	10.68 ± 0.24	9.78	9.24 - 10.17	9.62 ± 0.40
Percent of head length (HL):									
Cleithral width [Cleitr_w]	92.08 - 102.96	95.74 ± 3.45	98.23 - 107.73	103.42 ± 2.52	94.32 - 100.79	97.47 ± 2.20	81.06	87.27 - 97.44	92.37 ± 4.32
Head depth [Depth_head]	59.94 - 71.53	64.27 ± 3.61	63.00 - 70.02	66.61 ± 1.83	57.36 - 63.61	60.66 ± 1.92	64.29	56.82 - 62.62	60.89 ± 2.74
Snout length [Snouth_l]	57.74 - 61.72	59.19 ± 1.43	58.51 - 62.68	61.00 ± 1.12	56.90 - 60.53	58.02 ± 1.07	54.04	54.92 - 57.91	56.23 ± 1.52
Orbital diameter [Orbit_d]	18.10 - 20.54	19.22 ± 0.78	14.97 - 17.12	16.09 ± 0.67	16.41 - 20.05	18.50 ± 0.93	21.48	15.50 - 16.94	16.16 ± 0.61
Interorbital length [Interorb_l]	41.15 - 45.48	43.08 ± 1.43	40.60 - 47.10	45.48 ± 1.65	41.09 - 47.64	43.34 ± 1.85	39.26	38.42 - 41.34	39.37 ± 1.33
Other percentages:									
Caudal-peduncule depth % of interdorsal length	51.88 - 60.41	56.48 ± 2.64	50.66 - 67.87	58.04 ± 4.60	58.29 - 66.67	62.54 ± 3.10	57.07	50.05 - 56.54	52.47 ± 2.89
Caudal-peduncule depth % of peduncule length	30.39 - 35.89	33.21 ± 1.62	32.14 - 39.10	35.16 ± 1.87	34.38 - 38.97	36.23 ± 1.47	31.04	30.40 - 34.22	31.94 ± 1.62
Dentary length % of interorbital length	33.33 - 41.91	35.95 ± 3.02	25.27 - 29.88	27.12 ± 1.38	- -	- -	27.06	27.11 - 31.38	29.57 ± 1.82
Counts									
Number of premaxillary teeth (L)	21 - 27	24 ± 2	21 - 29	25 ± 2	- -	- -	-	24 - 26	25 ± 1
Number of premaxillary teeth (R)	20 - 27	23 ± 3	21 - 31	25 ± 2	- -	- -	-	24 - 26	25 ± 1
Number of dentary teeth (L)	20 - 24	22 ± 2	16 - 25	22 ± 3	- -	- -	-	24 - 26	25 ± 1
Number of dentary teeth (R)	18 - 26	21 ± 3	17 - 27	23 ± 3	- -	- -	-	23 - 28	25 ± 1
Number of plates in the lateral series (L)	26 - 27	27 ± 0	26 - 27	26 ± 1	- -	- -	27	25 - 27	27 ± 1
Number of plates in the lateral series (R)	26 - 28	27 ± 1	26 - 27	26 ± 1	- -	- -	27	27 - 27	27 ± 0
Number of predorsal rows of plates	3 - 3	3 ± 0	3 - 3	3 ± 0	- -	- -	3	3 - 3	3 ± 0
Number of dorsal plates	7 - 8	8 ± 0	8 - 9	9 ± 1	- -	- -	-	8 - 8	8 ± 0
Number of plates between dorsal and adipose fins	7 - 8	8 ± 1	6 - 7	6 ± 0	- -	- -	7	7 - 8	7 ± 1
Number of plates between adipose and caudal fins	5 - 8	6 ± 1	7 - 8	8 ± 0	- -	- -	7	8 - 8	8 ± 0
Number of plates between anal and caudal fins	12 - 14	13 ± 1	13 - 15	14 ± 0	- -	- -	-	14 - 15	4 ± 1

Table I. - Continued.

Species	*Hypostomus plecostomus*		*Hypostomus watwata*					
Former identification	All forms & populations		*H. watwata*					
Locality & acronym of population			Oyapok (WOya)		Cayenne (WCay)		Kourou (WKou)	
N	158		4		20		10	
	range	mean ± sd	range	mean ± sd	range	mean ± sd	range	mean ± sd
Morphometry								
Standard length (SL)	56.00 - 249.80	159.65 ± 49.44	179.50 - 283.90	245.70 ± 48.73	258.30 - 390.00	324.31 ± 35.52	134.00 - 352.00	231.14 ± 71.26
Percents of SL:								
Predorsal length [Predors_l]	37.45 - 44.71	40.23 ± 1.46	36.25 - 39.11	37.58 ± 1.24	34.58 - 39.58	36.77 ± 1.12	35.57 - 39.93	37.58 ± 1.20
Head length [Head_l]	30.34 - 41.39	33.22 ± 1.83	29.27 - 32.03	30.58 ± 1.20	27.72 - 32.49	30.03 ± 1.26	29.46 - 33.06	30.93 ± 1.28
Dorsal-fin spine [Dspine_l]	27.80 - 41.86	34.29 ± 2.62	30.45 - 37.21	32.81 ± 3.17	0.00 - 32.29	27.48 ± 6.77	29.05 - 34.84	31.24 ± 2.15
Interdorsal length [Interdor_l]	15.15 - 21.16	17.87 ± 1.28	19.41 - 21.90	20.64 ± 1.16	19.55 - 22.90	21.25 ± 0.89	16.67 - 22.78	20.69 ± 1.80
Caudal-peduncule length [Peduncl_l]	24.88 - 36.76	31.18 ± 1.73	34.43 - 36.63	35.22 ± 1.04	33.37 - 38.05	35.54 ± 1.35	33.77 37.81	35.42 ± 1.28
Caudal-peduncule depth [Peduncl_d]	9.24 - 11.76	10.46 ± 0.47	8.90 - 9.47	9.15 ± 0.27	7.54 - 8.85	8.36 ± 0.35	8.15 - 9.27	8.58 ± 0.31
Percent of head length (HL):								
Cleithral width [Cleitr_w]	76.51 - 107.73	97.78 ± 5.72	94.26 - 98.81	96.56 ± 2.46	84.69 - 99.63	93.07 ± 3.48	89.62 - 96.27	93.99 ± 2.10
Head depth [Depth_head]	49.75 - 75.97	63.19 ± 4.77	59.59 - 63.90	61.30 ± 2.08	55.63 - 65.54	61.16 ± 2.31	60.88 - 65.70	62.04 ± 1.49
Snout length [Snouth_l]	46.98 - 62.68	58.75 ± 2.32	55.48 - 57.03	56.23 ± 0.64	50.80 - 57.38	55.69 ± 1.61	55.35 - 57.84	56.98 ± 0.83
Orbital diameter [Orbit_d]	14.16 - 24.16	17.17 ± 2.07	12.15 - 14.78	13.24 ± 1.11	11.26 - 14.16	13.04 ± 0.77	13.02 - 17.60	15.27 ± 1.60
Interorbital length [Interorb_l]	37.91 - 47.64	42.51 ± 1.92	45.61 - 47.69	46.71 ± 1.03	41.27 - 47.88	44.64 ± 1.75	44.71 - 48.50	46.37 ± 1.17
Other percentages:								
Caudal-peduncule depth % of interdorsal length	47.46 - 72.94	58.81 ± 4.93	40.65 - 47.49	44.43 ± 3.01	32.92 - 43.87	39.42 ± 2.61	35.79 - 55.64	41.92 ± 5.56
Caudal-peduncule depth % of peduncule length	28.04 - 42.63	33.64 ± 2.46	24.42 - 27.51	25.99 ± 1.27	19.81 - 25.75	23.56 ± 1.44	21.56 - 27.46	24.28 ± 1.57
Dentary length % of interorbital length	23.20 - 41.91	29.95 ± 3.23	26.74 - 28.76	27.46 ± 0.90	24.40 - 34.15	28.01 ± 2.20	25.07 - 30.91	28.01 ± 1.54
Counts								
Number of premaxillary teeth (L)	19 - 45	30 ± 5	24 - 30	27 ± 3	23 - 29	27 ± 2	20 - 29	26 ± 3
Number of premaxillary teeth (R)	20 - 45	29 ± 5	24 - 30	27 ± 4	21 - 30	26 ± 3	21 - 28	26 ± 3
Number of dentary teeth (L)	16 - 41	28 ± 6	22 - 31	26 ± 5	24 - 30	28 ± 2	16 - 31	27 ± 5
Number of dentary teeth (R)	17 - 41	29 ± 6	23 - 32	27 ± 5	20 - 32	27 ± 4	22 - 29	27 ± 2
Number of plates in the lateral series (L)	25 - 28	27 ± 0	26 - 26	26 ± 0	26 - 27	27 ± 1	26 - 27	27 ± 1
Number of plates in the lateral series (R)	26 - 28	27 ± 0	26 - 26	26 ± 0	26 - 27	27 ± 1	26 - 27	27 ± 1
Number of predorsal rows of plates	2 - 3	3 ± 0	3 - 3	3 ± 0	3 - 3	3 ± 0	3 - 3	3 ± 0
Number of dorsal plates	7 - 9	9 ± 1	7 - 9	8 ± 1	7 - 9	8 ± 1	7 - 8	8 ± 1
Number of plates between dorsal and adipose fins	6 - 8	7 ± 1	6 - 7	7 ± 1	6 - 8	7 ± 1	6 - 7	7 ± 1
Number of plates between adipose and caudal fins	5 - 9	8 ± 1	8 - 9	9 ± 1	7 - 9	8 ± 1	8 - 9	9 ± 1
Number of plates between anal and caudal fins	12 - 15	14 ± 1	14 - 14	14 ± 0	13 - 14	14 ± 1	13 - 14	14 ± 1

Table I. - Continued.

Species	*Hypostomus watwata*							
Former identification	*H. watwata*							
Locality & acronym of population	Sinnamary (WSin)		Mana + Maroni (WMar)		Maroni (WMarB)*		Suriname (WPuK)	
N	9		14		4		14	
	range	mean ± sd	range	mean ± sd	range	mean ± sd	range	mean ± sd
Morphometry								
Standard length (SL)	185.90 - 295.00	241.14 ± 39.38	120.10 372.00	232.71 74.47	130.00 - 253.00	170.75 ± 56.23	107.90 - 141.10	126.70 ± 11.94
Percents of SL:								
Predorsal length [Predors_l]	35.80 - 38.33	37.18 ± 1.04	35.76 - 39.88	38.46 ± 1.33	37.39 - 40.92	39.57 ± 1.54	39.26 - 40.59	39.94 ± 0.54
Head length [Head_l]	28.37 - 30.93	29.75 ± 0.96	29.24 - 33.14	31.81 ± 1.07	30.00 - 33.23	32.11 ± 1.44	32.25 - 34.57	33.43 ± 0.89
Dorsal-fin spine [Dspine_l]	29.75 - 33.54	31.51 ± 1.29	27.80 - 36.25	32.42 ± 2.52	31.07 - 33.00	32.44 ± 0.92	32.33 - 34.07	33.20 ± 1.23
Interdorsal length [Interdor_l]	19.63 - 23.63	21.81 ± 1.26	17.82 - 22.77	20.63 ± 1.22	19.00 - 20.50	19.62 ± 0.64	18.14 - 19.37	18.71 ± 0.47
Caudal-peduncule length [Peduncl_l]	33.00 - 35.66	34.73 ± 0.81	33.14 - 36.14	34.51 ± 1.13	31.50 - 33.99	33.08 ± 1.14	32.96 - 33.95	33.35 ± 0.41
Caudal-peduncule depth [Peduncl_d]	8.09 - 8.76	8.38 ± 0.24	8.80 - 9.53	9.15 ± 0.25	8.42 - 9.36	8.83 ± 0.43	9.22 - 9.78	9.56 ± 0.23
Percent of head length (HL):								
Cleithral width [Cleitr_w]	91.29 - 99.28	94.30 ± 2.75	89.08 - 99.59	95.38 ± 2.49	90.38 - 98.55	94.80 ± 3.44	92.23 - 96.96	95.22 ± 1.94
Head depth [Depth_head]	56.91 - 64.28	61.14 ± 2.26	58.69 - 66.53	61.83 ± 2.13	58.10 - 61.53	59.64 ± 1.56	59.95 - 62.18	60.78 ± 0.84
Snout length [Snouth_l]	55.75 - 58.67	57.38 ± 1.03	51.54 - 58.16	56.34 ± 1.65	55.32 - 57.18	56.32 ± 0.96	55.22 - 57.58	56.07 ± 0.94
Orbital diameter [Orbit_d]	13.50 - 17.60	15.21 ± 1.18	11.36 - 18.09	14.26 ± 1.99	13.18 - 18.06	16.00 ± 2.07	14.29 - 14.95	14.62 ± 0.25
Interorbital length [Interorb_l]	43.44 - 46.44	45.00 ± 0.97	40.19 - 47.95	45.95 ± 1.98	43.67 - 45.60	44.70 ± 0.82	45.09 - 47.91	46.98 ± 1.17
Other percentages:								
Caudal-peduncule depth % of interdorsal length	36.28 - 41.64	38.53 ± 2.05	39.43 - 53.48	44.52 ± 3.41	43.47 - 45.88	45.02 ± 1.09	49.58 - 53.13	51.11 ± 1.80
Caudal-peduncule depth % of peduncule length	23.46 - 24.84	24.14 ± 0.49	24.24 - 28.64	26.25 ± 1.41	24.77 - 29.71	26.75 ± 2.11	27.61 - 29.67	28.66 ± 0.95
Dentary length % of interorbital length	28.57 - 32.90	30.10 ± 1.38	26.83 - 31.06	28.60 ± 1.20	- -	- -	23.03 - 26.94	25.13 ± 1.78
Counts								
Number of premaxillary teeth (L)	24 - 34	30 ± 3	24 - 33	298 ± 3	- -	- -	11 - 26	20 ± 6
Number of premaxillary teeth (R)	22 - 35	31 ± 4	23 - 32	28 ± 3	- -	- -	19 - 27	22 ± 3
Number of dentary teeth (L)	20 - 33	29 ± 4	22 - 34	27 ± 3	- -	- -	18 - 27	22 ± 3
Number of dentary teeth (R)	23 - 33	29 ± 3	25 - 32	28 ± 2	- -	- -	18 - 26	21 ± 3
Number of plates in the lateral series (L)	25 - 26	26 ± 0	25 - 26	26 ± 0	- -	- -	26 - 26	26 ± 0
Number of plates in the lateral series (R)	26 - 26	26 ± 0	25 - 26	26 ± 0	- -	- -	26 - 26	26 ± 0
Number of predorsal rows of plates	3 - 3	3 ± 0	3 - 3	3 ± 0	- -	- -	3 - 3	3 ± 0
Number of dorsal plates	7 - 9	8 ± 1	7 - 8	8 ± 0	- -	- -	7 - 8	8 ± 0
Number of plates between dorsal and adipose fins	6 - 7	7 ± 0	6 - 7	6 ± 1	- -	- -	6 - 7	6 ± 0
Number of plates between adipose and caudal fins	8 - 9	8 ± 0	7 - 8	8 ± 0	- -	- -	8 - 8	8 ± 0
Number of plates between anal and caudal fins	13 - 14	14 ± 1	13 - 14	14 ± 0	- -	- -	14 - 14	14 ± 0

Table I. - End.

Species	*Hypostomus watwata*								
Former identification	*H. watwata*					*H. plecostomus*		All forms & populations	
Locality & acronym of population	Mouth of Suriname River *		Coppename + Saramacca (WCop)*		(Wneo)*	(Psyn2)	(Psyn3)		
N	4		4		1	2		86	
	range	mean ± sd	range	mean ± sd	neotype	paralectotypes		range	mean ± sd
Morphometry									
Standard length (SL)	113.00 - 217.00	162.25 ± 46.37	138.00 - 202.00	176.75 ± 30.41	260.00	81.40	82.00	107.90 - 390.00	240.90 ± 77.67
Percents of SL:		±							
Predorsal length [Predors_l]	37.56 - 41.26	39.94 ± 1.65	39.41 - 40.72	40.00 ± 0.57	37.04	44.10	41.59	34.58 - 44.10	37.96 ± 1.59
Head length [Head_l]	31.34 - 34.07	33.02 ± 1.25	31.63 - 33.91	32.92 ± 1.00	30.00	37.71	35.24	27.72 - 37.71	31.13 ± 1.62
Dorsal-fin spine [Dspine_l]	31.34 - 35.93	32.79 ± 2.12	32.97 - 34.73	34.07 ± 0.77	31.54	34.15	-	25.90 - 37.21	31.33 ± 2.55
Interdorsal length [Interdor_l]	19.71 - 20.99	20.48 ± 0.55	18.44 - 21.25	19.92 ± 1.48	20.19	19.10	18.90	16.67 - 23.63	20.71 ± 1.37
Caudal-peduncule length [Peduncl_l]	32.70 - 35.48	33.53 ± 1.32	32.99 - 34.41	33.46 ± 0.64	35.92	34.83	35.00	31.50 38.05	34.78 ± 1.38
Caudal-peduncule depth [Peduncl_d]	8.61 - 9.51	9.03 ± 0.37	9.06 - 9.50	9.25 ± 0.19	8.65	8.97	8.41	7.54 - 9.78	8.70 ± 0.50
Percent of head length (HL):									
Cleithral width [Cleitr_w]	90.91 - 97.65	93.97 ± 3.44	91.23 - 96.78	94.16 ± 2.70	98.97	85.34	87.20	84.69 - 99.63	94.28 ± 2.91
Head depth [Depth_head]	52.99 - 63.99	58.64 ± 5.11	57.05 - 64.95	61.50 ± 3.98	62.31	61.38	59.58	52.99 - 66.53	61.16 ± 2.43
Snout length [Snouth_l]	54.03 - 58.63	56.42 ± 2.27	54.70 - 59.42	57.08 ± 1.93	56.54	52.28	53.63	50.80 - 59.42	56.39 ± 1.47
Orbital diameter [Orbit_d]	13.97 - 17.66	15.71 ± 1.80	14.09 - 16.03	15.02 ± 0.92	13.72	17.92	17.99	11.26 - 18.09	14.34 ± 1.61
Interorbital length [Interorb_l]	42.67 - 47.57	45.39 ± 2.02	45.08 - 47.10	46.12 ± 0.89	44.87	43.81	44.64	40.19 - 48.50	45.52 ± 1.71
Other percentages:									
Caudal-peduncule depth % of interdorsal length	43.59 - 45.29	44.10 ± 0.80	43.33 - 50.32	46.61 ± 3.18	42.86	46.95	44.52	32.92 - 55.64	42.61 ± 4.60
Caudal-peduncule depth % of peduncule length	25.32 - 28.64	26.97 ± 1.44	26.62 - 28.57	27.65 ± 0.87	24.09	25.75	24.04	19.81 - 29.71	25.29 ± 2.07
Dentary length % of interorbital length	- -	- -	- -	- -	-	26.77	-	23.03 - 34.15	28.18 ± 2.01
Counts									
Number of premaxillary teeth (L)	- -	- -	- -	- -	-	-	-	11 - 34	27 ± 4
Number of premaxillary teeth (R)	- -	- -	- -	- -	23	23	-	19 - 35	27 ± 4
Number of dentary teeth (L)	- -	- -	- -	- -	-	-	-	16 - 34	27 ± 3
Number of dentary teeth (R)	- -	- -	- -	- -	25	25	-	18 - 33	27 ± 3
Number of plates in the lateral series (L)	- -	- -	- -	- -	-	-	-	25 - 27	26 ± 0
Number of plates in the lateral series (R)	- -	- -	- -	- -	25	25	-	25 - 27	26 ± 0
Number of predorsal rows of plates	- -	- -	- -	- -	-	-	-	3 - 3	3 ± 0
Number of dorsal plates	- -	- -	- -	- -	-	-	-	7 - 9	8 ± 1
Number of plates between dorsal and adipose fins	- -	- -	- -	- -	-	-	-	6 - 8	7 ± 1
Number of plates between adipose and caudal fins	- -	- -	- -	- -	-	-	-	7 - 9	8 ± 0
Number of plates between anal and caudal fins	- -	- -	- -	- -	-	-	-	13 - 14	14 ± 0

included in the analyses due to the small samples size and, for *H. corantijni* to a poor electrophoretic resolution that may lead to misinterpretation of the electrophoregrams. These samples were regarded only qualitatively, providing additional information to the species boundaries.

White skeletal muscle samples were taken from each specimen and frozen in liquid nitrogen immediately after collection and later stored at –80°C. Liver samples of some specimens were also preserved in the objective of electrophoregram interpretation. Preparation of protein extracts and electrophoretic procedures are detailed in Fisch-Muller *et al*. (2001). Staining for eight enzyme systems (Tab. II) follow Pasteur *et al*. (1987). The mobility of the enzymes was determined in separate side-by-side electrophoretic runs, and electromorphs of various loci were considered homologous if they exhibited the same mobility. The individual genotypes were inferred on the basis of the allozyme phenotypes following Pasteur *et al*. (1987) and Buth (1990). Enzyme abbreviations and locus nomenclature follow Shaklee *et al*. (1990). Alleles were designated alphabetically based on decreasing electrophoretic mobility. Data were analysed using TFPGA 1.3 (Miller, 1997). Genotype proportions at each polymorphic locus within a population were tested for deviation from Hardy-Weinberg equilibrium using Haldane's exact test (Haldane, 1954). A multiple testing correction procedure was applied to control for the False Discovery Rate (FDR) (Benjamini and Hochberg, 1995). Parameters used to estimate genetic variation of populations and species are: percentage of polymorphic loci at 95% (P0.95) and 99% (P0.99) criteria, and observed (Ho) and unbiased estimates of average heterozygosity (He) (Nei, 1978). Exact tests for population differentiation (Raymond and Rousset, 1995) were conducted using a contingency table approach and the Markov chain procedure on allelic frequencies of each locus at population and species levels, and the Fisher's Combined Probability test was computed as a global test over loci to determine the overall significance. Intraspecific and interspecific genetic distances were calculated using Nei's unbiased formulae adapted for small samples (Nei, 1978), which can give negative values. The genetic distances matrix was then submitted to an agglomerative hierarchical clustering analysis using the Unweighed Pair-Group Method with Arithmetic mean (UPGMA) (Sneath and Sokal, 1973) algorithm. The resulting tree was used as a graphical representation of the genetic distances to infer phenetic relationships between populations. To estimate robustness of the clusters, a non-parametric bootstrap analysis (Efron, 1979) was performed following Felsenstein's (1985) methodology using 10'000 pseudoreplicates. Only fixed allozymic differences at isozyme loci, which are hypothesized from observed allelic frequencies of the samples of populations, provide unequivocal identification of specimens and have been used as diagnostic markers of species according to Davis and Nixon (1992). In case of allopatry and in the absence of evidence from other type of data, a minimum of two fixed allozymic differences was necessary to recognize distinct species. Electrophoretic gels are preserved in MHNG together with photographs, and are available upon request.

Table II. - Enzymes names, abbreviations and Enzyme Commission numbers.

Enzymes	E.C. numbers
Creatine kinase (CK)	2.7.3.2
Glycerol-3-phosphate dehydrogenase (NAD+) (G3PDH)	1.1.1.8
Glucose-6-phosphate isomerase (GPI)	5.3.1.9
L-Lactate dehydrogenase (LDH)	1.1.1.27
Malate dehydrogenase (MDH)	1.1.1.37
Malic enzyme (NADP+) (MEP)	1.1.1.40
Mannose-6-phosphate isomerase (MPI)	5.3.1.8
Phosphoglucomutase (PGM)	5.4.2.2

RESULTS

Morphometry

Characteristics of the data set

No significant differences were observed between our measurements and those from Boeseman since the Wilcoxon matched pairs signed rank test failed to reject the null hypothesis (H0: $M_{CW} - Mm_B = 0$ *vs*. H1: $M_{CW} - Mm_B \neq 0$; V = 54, p-value = 0.6441). All available data were accordingly gathered into a single data set and submitted to the multivariate analyses. The between class inertia recorded by the DA represented 37.02% of the total inertia (sum of eigenvalues / matrix rank: 5.1835 / 14 = 0.3702). The non-parametric version of the Pillai test (Fig. 1D) was highly significant with none of the null hypothesis sampling distribution of randomized values greater than the observed value of between class inertia ($X_{obs} = 0.3702$; $p_{Xrand} \geq p_{Xobs} = 0.0001$). Significant differences between groups were thus present in the data, and these differences were not due to chance.

Discriminant analysis of the different populations and species

Morphometric data were mainly structured on the first two axes of DA (Fig. 1C) that explained 35.84% of the total between-class inertia (18.46% for axis 1 and 17.38% for axis 2). The first axis split the different populations and species of *Hypostomus* into four main groups (Fig. 1A). On the negative side, the first one corresponded to a group mixing five Surinamese species described by Boeseman, followed by a second group comprising different populations of *H. gymnorhynchus* and their close morphological relatives. On the positive side, a first group com-

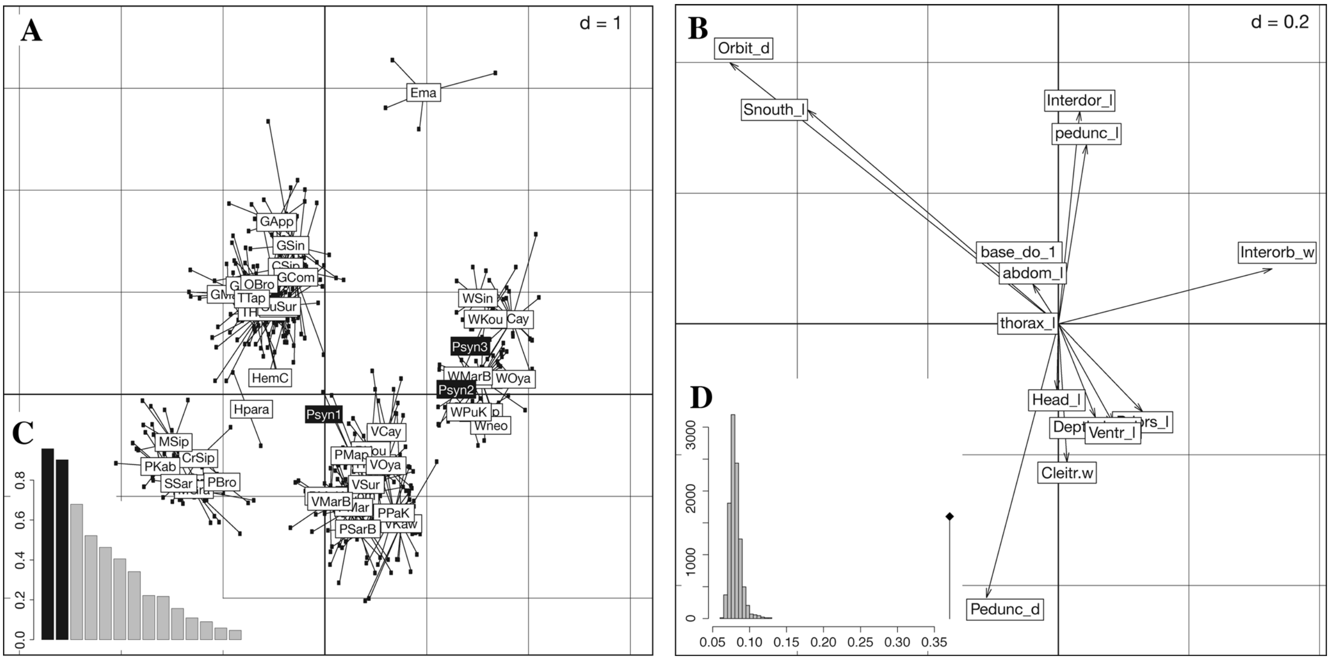

Figure 1. - Linear Discriminant Analysis of the different populations and species representing most of the Guianese *Hypostomus*. **A**: Projection of 523 specimens distributed in 43 groups, and *a posteriori* group assignment of the three Linnean syntypes onto the first factorial plane of the DA; populations and species labelled as in Material examined and table I. **B**: Projection of the discriminant factors onto the first factorial plane of the DA; variables labelled as in table I. **C**: Eigenvalues of the DA. **D**: Non parametric Pillai test.

prised different populations of *H. plecostomus* and *H. ventromaculatus*, followed by a second group comprising all populations of *H. watwata*. The second axis split *H. emarginatus* from the groups comprising the different populations of *H. gymnorhynchus* and relatives plus all populations of *H. watwata* on positive values, and the groups comprising the five different species of Boeseman and the different populations of *H. plecostomus* and *H. ventromaculatus* on negatives values. Four species groups are accordingly recognized and named: Boeseman (for five species described by Boeseman), *gymnorhynchus*, *plecostomus*, and *watwata* groups. The species *H. emarginatus* was perfectly distinct from all other Guianese species, whereas the two populations of *H. hemiurus* appeared intermediary between the Boeseman and *gymnorhynchus* groups. On the negative side of axis 1, the Boeseman group corresponded to high values for maximum orbital diameter, and snout length (Fig. 1B). It comprised five representatives of the Surinamese species of *Hypostomus* described by Boeseman (inc. type material): *H. macrophthalmus*, *H. pseudohemiurus*, *H. crassicauda*, *H. paucimaculatus*, *H. saramaccensis*, and two populations of *H. micromaculatus* (Brokopondo and Gran Rio). On the positive side of axis 1, the *watwata* group corresponded to high values for the interorbital width (Fig. 1B). It consisted in the Guianese populations of the nominal species: Cayenne, Kourou, Sinnamary, Maroni, Suriname, Oyapock, Berbice (Boeseman's neotype of *Acipenser plecostomus*), and Coppename Rivers, plus the population from Pulp Creek (lower Suriname River). On the positive side of axis 2, *H. emarginatus* and the *gymnorhynchus* group corresponded to high values for the interdorsal and caudal peduncle lengths (Fig. 1B). The *gymnorhynchus* group comprised different populations of the nominal species (Approuague, Sinnamary, Comté, Mana and upper Maroni Rivers), plus the representatives (inc. type material) of *H. tapanahoniensis*, *H. corantijni*, *H. nickeriensis*, *H. occidentalis*, *H. surinamensis*, and *H. sipaliwinii*. On the negative side of axis 2 the *plecostomus* group corresponded to high values for the caudal peduncle depth, and in less important contributions to the cleithral width (Fig. 1B). The *plecostomus* group comprised a mix of different populations of *H. plecostomus* (Paulus Creek-lower Suriname River, Saramacca River, Marshall Creek-lower Suriname River, Suriname River, and Mapana Creek-lower Commewijn River), of *H. ventromaculatus* including *H.* cf. *ventromaculatus* (sensu Le Bail, 2000) [Oyapock, Kaw, Kourou, Cayenne, Maroni, Commewijn, and Suriname (type material) Rivers], and a population identified as *H. hemiurus* from lower Essequibo River. The two other populations of *H. hemiurus* were poorly characterized in negative values on the first axis.

Discriminant model and a posteriori assignment of Linnean types

The cross validation procedure used to validate the discriminant functions, and accordingly their predictive abilities, recovered a rate of false assignment of 36% considering the

grouping by population. By grouping the different populations of a given species into species groups, this rate dropped to 8% of false assignment. These wrong assignments concerned however mainly the Boeseman group. The model was thus considered valid at the specific level, and cautiously at the population level. The *a posteriori* class assignment predicted the first putative syntype of *H. plecostomus* (Psyn1: SL = 57.8 mm) as a member of *H. plecostomus* Mapana Creek, lower Commewijn River using either all discriminant functions (n = 14) or only the two first ones. The second putative syntype of *H. plecostomus* (Psyn2: SL = 81.40 mm) was assigned to *H. watwata*, Maroni River, using either 14 or 2 discriminant functions. The third putative syntype of *H. plecostomus* (Psyn3: SL = 82.00 mm) was assigned to *H. watwata*, Kourou River, using the 14 discriminant functions, and to *H. watwata*, Maroni River, using the discriminant functions 1 and 2. Since these two syntypes (Psyn2 and Psyn3) belonged to the same lot, it was very unlikely that one was collected in Maroni River and the second in Kourou River. The two first discriminant functions appeared thus as the best predictors, and class' scores onto the two first axes of the DA were consequently used for the cluster analysis.

Cluster analysis of the different populations and species

The clustering structure of the morphometric dataset using WPGMA was high (agglomerative coefficient = 0.91). The WPGMA tree (Fig. 2) recovered five clusters corresponding to the four morphological groups previously defined plus *H. emarginatus*. The first cluster only comprised *H. emarginatus*. The second cluster grouped all populations of *H. watwata* plus syntypes 2 and 3 of *H. plecostomus*. This cluster was statistically highly supported by both AU and BP p-values (99% AU / 99% bootstrap), as well as all internal positions including the nested positions of these two syntypes within the *watwata* group (95% AU / 94% bootstrap for syntype 2, and 90% AU / 78% bootstrap for syntype 3). The morphological group *watwata* was thus morphologically homogeneous and well structured. The next cluster comprised all species and populations constituting the *gymnorhynchus* group. This cluster was also highly supported (100% AU / 100% bootstrap) as well as most of its internal relationships. Like the *watwata* group, the *gymnorhynchus* group was morphologically homogeneous and well structured. The fourth cluster grouped all populations and species constituting the *plecostomus* group, including the syntype 1. This cluster was also strongly supported (91% AU / 71% bootstrap) but fell out of the bootstrap 95% confidence interval. This cluster comprised more variability, and only subsamples were comprised within the confidence interval such as *H. ventromaculatus* from Kaw River and *H. plecostomus* from Paulus Creek-lower Suriname River (100% AU / 100% bootstrap), *H. plecostomus* from Marshall Creek, and the

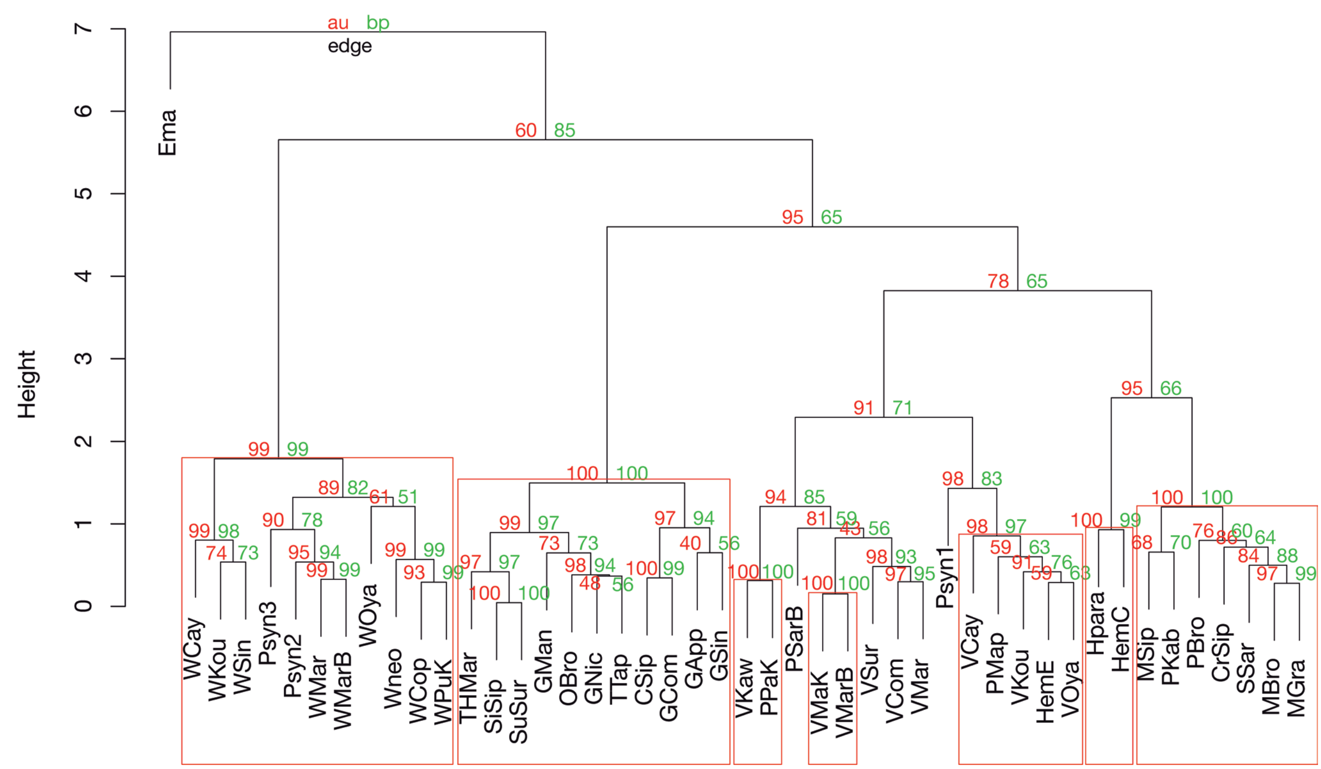

Figure 2. - WPGMA tree performed on the resulting scores of the DA with multiscale bootstraps analyses. Populations and species labelled as in Material examined and table I; agglomerative coefficient = 0.91; cluster supports are reported above nodes: left approximately unbiased (au) and right bootstrap probability (bp); squares represent confidence intervals at 95% bp.

Table III. - Observed allelic frequencies and measures of genetic diversity at population and species (bold) levels, for 18 samples of populations of *Hypostomus* from French Guiana and Suriname. *H. tapa*: *H. tapanahoniensis*. N: average sample size; P0.95, P0.99: percentage of polymorphic loci at 95% and 99% criterions; Ho: observed heterozygosity; He: expected heterozygosity (Nei, 1978). Dark grey areas indicate species's diagnostic alleles. Light grey area indicates no locus expression detected for the species.

	Species	*Hypostomus plecostomus*									*Hypostomus watwata*		
Former identification		*H.* cf. *ventromaculatus*				*H. ventromaculatus*		*H. plecostomus*			*H. watwata*		
Loci	Alleles	Oyapock	Kaw	Mahury	Kourou	Maroni	Suriname 1	Suriname 2	Saramacca	**Total**	Oyapock	Cayenne	Sinnamary
Ck	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	**1.000**	-	-	-
	b	-	-	-	-	-	-	-	-	-	1.000	1.000	1.000
G3pdh	a	-	-	-	-	-	-	-	-	-	1.000	1.000	1.000
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	**1.000**	-	-	-
Gpi-A	a	-	-	-	-	-	-	-	-	-	-	-	-
	b	-	-	-	-	1.000	-	-	-	**1.000**	-	1.000	-
	c	-	-	-	-	-	-	-	-	-	-	-	-
	d	-	-	-	-	-	-	-	-	-	-	-	-
Gpi-B	a	-	-	-	-	-	-	-	-	-	-	-	-
	b	-	-	-	-	-	-	-	-	-	-	-	-
	c	-	-	-	0.350	0.143	-	-	-	**0.056**	-	-	-
	d	1.000	1.000	1.000	0.650	0.821	1.000	1.000	1.000	**0.939**	1.000	1.000	1.000
	e	-	-	-	-	0.036	-	-	-	**0.005**	-	-	-
Ldh-1	a	-	-	-	-	-	-	-	-	-	-	-	-
	b	1.000	1.000	1.000	1.000	1.000	1.000	0.971	0.833	**0.986**	-	-	-
	c	-	-	-	-	-	-	0.029	0.167	**0.014**	-	-	-
Ldh-2	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	**1.000**	-	-	-
	b	-	-	-	-	-	-	-	-	-	1.000	1.000	1.000
Mdh	a	1.000	1.000	1.000	0.850	1.000	1.000	0.971	1.000	**0.980**	1.000	1.000	1.000
	b	-	-	-	0.150	-	-	-	-	**0.015**	-	-	-
	c	-	-	-	-	-	-	0.029	-	**0.005**	-	-	-
Mep-1	a	-	-	-	-	-	-	-	-	-	-	-	0.583
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	**1.000**	1.000	1.000	0.417
Mep-2	a	0.605	0.607	1.000	1.000	0.750	1.000	1.000	1.000	**0.830**	-	-	0.083
	b	0.395	0.393	-	-	0.250	-	-	-	**0.170**	1.000	1.000	0.917
	c	-	-	-	-	-	-	-	-	-	-	-	-
Mpi	a	0.575	0.546	0.583	0.550	0.607	0.546	0.647	0.333	**0.576**	0.250	0.333	0.417
	b	0.425	0.455	0.417	0.450	0.393	0.455	0.353	0.667	**0.424**	0.750	0.667	0.583
Pgm	a	-	0.143	-	-	-	-	-	-	**0.020**	0.375	0.056	0.500
	b	1.000	0.857	1.000	1.000	1.000	1.000	1.000	1.000	**0.980**	0.625	0.944	0.500
N		17.500	12.500	7.800	10.000	12.818	10.900	16.900	2.900	**84.182**	4.000	8.100	6.000
P0.95		20.000	30.000	10.000	30.000	27.273	10.000	10.000	20.000	**27.273**	22.222	20.000	44.444
P0.99		20.000	30.000	10.000	30.000	27.273	10.000	30.000	20.000	**54.546**	22.222	20.000	44.444
Ho		0.061	0.105	0.050	0.150	0.110	0.036	0.071	0.100	**0.077**	0.083	0.056	0.241
He		0.099	0.127	0.053	0.127	0.109	0.052	0.059	0.087	**0.091**	0.107	0.058	0.197

Table III. - Continued.

Species		*Hypostomus watwata*				*Hypostomus gymnorhynchus*				
Former identification		*H. watwata*				*H. gymnorhynchus*			*H. tapa*	
Loci	Alleles	Mana	Maroni	Suriname	**Total**	Approuague	Mahury	Sinnamary	Maroni	**Total**
Ck	a	-	-	-	-	1.000	1.000	1.000	1.000	**1.000**
	b	1.000	1.000	1.000	**1.000**	-	-	-	-	-
G3pdh	a	1.000	1.000	1.000	**1.000**	1.000	1.000	1.000	1.000	**1.000**
	b	-	-	-	-	-	-	-	-	-
Gpi-A	a	-	-	0.143	**0.111**	-	-	-	-	-
	b	-	-	0.857	**0.889**	-	-	-	-	-
	c	-	-	-	-	1.000	0.929	1.000	0.857	**0.948**
	d	-	-	-	-	-	0.071	-	0.143	**0.052**
Gpi-B	a	-	-	-	-	-	-	-	0.071	**0.017**
	b	-	-	-	-	1.000	1.000	1.000	0.929	**0.983**
	c	-	-	0.125	**0.024**	-	-	-	-	-
	d	1.000	1.000	0.875	**0.976**	-	-	-	-	-
	e	-	-	-	-	-	-	-	-	-
Ldh-1	a	-	-	-	-	1.000	-	1.000	1.000	**1.000**
	b	-	-	-	-	-	-	-	-	-
	c	-	-	-	-	-	-	-	-	-
Ldh-2	a	-	-	-	-	-	-	-	-	-
	b	1.000	1.000	1.000	**1.000**	1.000	-	1.000	1.000	**1.000**
Mdh	a	1.000	1.000	1.000	**1.000**	1.000	1.000	1.000	1.000	**1.000**
	b	-	-	-	-	-	-	-	-	-
	c	-	-	-	-	-	-	-	-	-
Mep-1	a	-	-	-	**0.088**	-	-	-	-	-
	b	1.000	1.000	1.000	**0.913**	1.000	1.000	1.000	1.000	**1.000**
Mep-2	a	-	-	-	**0.013**	-	-	-	-	-
	b	1.000	1.000	1.000	**0.988**	-	-	-	-	-
	c	-	-	-	-	1.000	1.000	1.000	1.000	**1.000**
Mpi	a	0.625	0.550	0.375	**0.427**	1.000	1.000	1.000	1.000	**1.000**
	b	0.375	0.450	0.625	**0.573**	-	-	-	-	-
Pgm	a	0.500	0.350	0.250	**0.305**	1.000	1.000	-	-	**0.552**
	b	0.500	0.650	0.750	**0.695**	-	-	1.000	1.000	**0.448**
N		3.889	10.000	7.900	**37.500**	8.909	7.000	6.000	6.727	**27.364**
P0.95		22.222	22.222	40.000	**40.000**	0.000	11.111	0.000	18.182	**18.182**
P0.99		22.222	22.222	40.000	**60.000**	0.000	11.111	0.000	18.182	**27.273**
Ho		0.083	0.133	0.154	**0.135**	0.000	0.016	0.000	0.039	**0.013**
He		0.123	0.111	0.140	**0.137**	0.000	0.016	0.000	0.037	**0.058**

type series of *H. ventromaculatus* (100% AU / 100% bootstrap), and the populations of *H. ventromaculatus* from Cayenne, Kourou, and Oyapock Rivers, the population of *H. plecostomus* from Mapana Creek-lower Commewijn River, and the population of *H. hemiurus* from lower Essequibo River (98% AU / 97% bootstrap). The *plecostomus* group appeared thus morphologically less well structured than the previous groups. The last cluster comprised two highly supported groups, one made of two populations of *H. hemiurus* (100% AU / 99% bootstrap), and a second comprising the species of the Boeseman group (100% AU / 100% bootstrap). The Boeseman group displayed high supports in its internal relationships and the two populations of *H. micromaculatus* clustered together reinforcing the conclusion of a group morphologically well structured.

Allozyme electrophoresis

Enzymatic polymorphism

The staining of eight enzyme systems (Tab. II) in 18 populations of *Hypostomus* allowed the scoring of 30 alleles encoded by 11 putative gene loci. The surveyed loci and the observed allelic frequencies for each sample of population

are presented in table III. No allele was detected for following cases: locus *Gpi-A* in *H. plecostomus* group except one specimen from Maroni, and in *H. watwata* group except two specimens from Cayenne, and locus *Ldh-1* in all *H. watwata* group. None of the 11 studied loci was found invariant, as they had from two (*Ck*, *Mep-1*, *Mpi* and *Pgm*) to five (*Gpi-B*) alternative alleles in the total sampling. None of the polymorphic loci for each population showed deviation to Hardy-Weinberg equilibrium expectations except *Mep-2*, that showed a significant deviation ($p = 0.004$; $cp_{(FDR)} = 0.152$) for the population of *H. ventromaculatus* from Oyapock (*H. plecostomus* group), with an excess of homozygotes. However, after correction for False Discovery Rate, this test could have been significant only by chance. In addition, this population appeared in Hardy-Weinberg equilibrium at its second polymorphic locus, *Mpi*.

Fixed allelic differences and species distinction

Comparison of allelic composition at each locus indicated that all populations identified as *H. plecostomus* group with morphology were fixed, in regards to *H. gymnorhynchus* and *H. watwata* groups, for distinctive and diagnostic alleles at three loci: *G3pdh*, *Ldh-1* and *Ldh-2* (Tab. III). However, at the species group level, no fixed allelic difference was found between populations preliminary identified as *Hypostomus* cf. *ventromaculatus*, *H. ventromaculatus* and *H. plecostomus* (Tab. III), ranging from the Oyapock to the Saramacca. The absence of any fixed allelic difference provided additional evidence that all these populations represent a single species: *H. plecostomus*. All analysed populations of *H. watwata* (*H. watwata* group), from the Oyapock to the Suriname basins, showed also a unique and exclusive allele at locus *Ck*, confirming the specific identity of *H. watwata*. Finally, *Hypostomus gymnorhynchus* group, including three populations of *H. gymnorhynchus* and one of *H. tapanahoniensis*, had fixed allelic differences with both other species (*H. plecostomus* and *H. watwata*) at no fewer than four loci: *Gpi-A*, *Gpi-B*, *Ldh-1*, and *Mep-2*. In addition alleles at these four loci are unique in our sampling. At *H. gymnorhynchus* group level, one fixed allelic difference was observed for locus *Pgm* between two pairs of populations: *H. gymnorhynchus* from Approuague and Mahury, both with allele *Pgm-a*, and *H. gymnorhynchus* from Sinnamary plus *H. tapanahoniensis* from Maroni, both showing allele *Pgm-b*. These clusters did not correspond to the two putative morphological species of the *H. gymnorhynchus* group. In the clear absence of morphologic evidence, a single fixed allelic difference is not sufficient to consider these two groups of allopatric populations as distinct species. In addition, the two alleles alternatively present were not unique in the sampling, as one of them was also found in *H. plecostomus* (*Pgm-a*), and both in *H. watwata*, showing that they cannot constitute diagnostic characters.

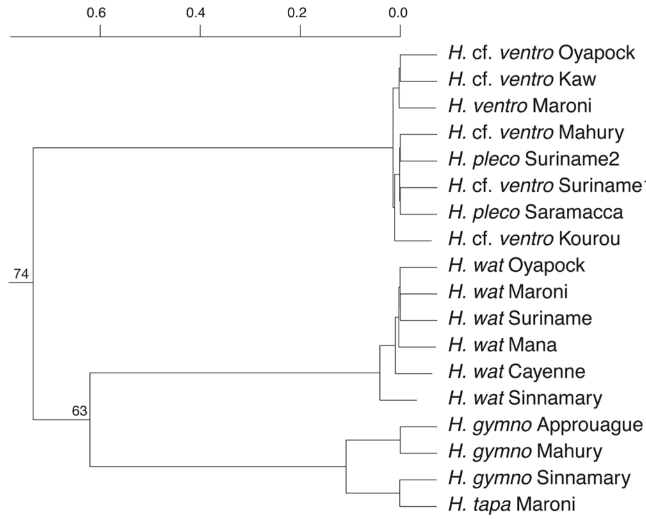

Figure 3. - UPGMA dendrogram of unbiased Nei's genetic distances (Nei, 1978) between 18 samples of populations of *Hypostomus* from French Guiana and Suriname. Negative branches not allowed. Agglomerative coefficient = 0.99. Only bootstrap values above 50 are reported.

Thus, in the 18 populations analysed, a total of eight loci can be considered as diagnostic markers for three distinct species, *H. plecostomus* (including *H. ventromaculatus* and *H.* cf. *ventromaculatus*), *H. watwata,* and *H. gymnorhynchus* (including *H. tapanahoniensis*). Exact tests for population differentiation between each pair of the three species confirmed overall significant differences in allele frequencies ($p = 0.000$ for each analysis). Nei's unbiased genetic distances between all pairs of populations ranged from -0.008 to 1.057. They are graphically summarized by an UPGMA dendrogram (Fig. 3), showing a clear grouping of the different populations into three clusters corresponding to the three species. Genetic distances were 0.558 between *H. plecostomus* and *H. watwata*, 0.933 between *H. plecostomus* and *H. gymnorhynchus*, and 0.624 between *H. watwata* and *H. gymnorhynchus*. Genetic identities between the species took the following respective values: 0.572, 0.393, and 0.536.

Besides allelic divergences, a difference in enzyme expression was observed for all populations of *H. watwata*, for which no product corresponding to *Ldh-1* activity was revealed in contrast to each population of *H. plecostomus* and *H. gymnorhynchus*. The two single specimens from Mahury and from Kourou (not included in population analyses) showed same allelic characteristics as all other *H. watwata* for the different loci surveyed, confirming their identification.

Intraspecific variation

Five rare alleles that appear exclusive to five populations were found: *Gpi-A-a* in *H. watwata* from Suriname, *Gpi-B-e* in *H. plecostomus* from Maroni, *Mdh-B-b* in *H. plecostomus* from Kourou, *Mdh-B-c* in *H. plecostomus* from Suriname 2 (Paulus Creek), and *Mep-1-a* in *H. watwata* from Sinnamary (Tab. III). Parameters estimating genetic variation are indicated in table III. At population level, proportion of polymorphic loci (whatever the criteria) ranged from zero in two populations of *H. gymnorhynchus* (Approuague and Sinnamary) to 44.4% in *H. watwata* from Sinnamary, and observed and unbiased estimates of average heterozygosity ranged respectively from zero to 0.241 and to 0.197 in the same populations.

The hypothesis of an absence of population differentiation between each of the eight populations of *Hypostomus plecostomus* was rejected in all cases except two: Oyapock and Kourou (p = 0.006), and Kaw and Kourou (p = 0.014), two pairs of populations that appeared differentiated on the base of their allelic frequencies. Genetic distances varied from -0.003 to 0.031, the most divergent populations being Kaw and Kourou. Percentage of polymorphic loci ranged from 10 to 30%, the most polymorph populations according to 95% criterion being Kaw and Kourou. Expected heterozygosity (He) ranged from 0.052 for Suriname 1 (Paramaribo) to 0.127 for Kaw and Kourou populations. At species level, expected heterozygosity was 0.091.

No overall significant population differentiation was found between the six populations of *H. watwata* ($0.087 \leq p \leq 1.000$), the species being thus genetically totally homogeneous. Genetic distances varied from -0.008 (Mana and Maroni) to 0.058 (Cayenne and Sinnamary). Percentage of polymorphic loci ranged from 20 to 44% and expected heterozygosity ranged from 0.058 to 0.197, Cayenne being the less variable and Sinnamary the most variable populations according to these parameters.

Despite a fixed allelic difference between two pairs of populations (see above), *H. gymnorhynchus* showed no significant population differentiation ($0.242 \leq p \leq 1.000$). Genetic distances between populations varied from 0.000 (Approuague and Mahury) to 0.120 (Mahury and Maroni). Out of the four populations analysed, two showed no polymorphic locus (Approuague and Sinnamary). The most polymorph population was that of Maroni ($P_{0.95}$ = 18.18; He = 0.037).

***Hypostomus plecostomus* (Linnaeus, 1758)**

(Figs 4, 5, 7A, 8A-B, 10; Tabs I, III)

Acipenser plecostomus Linnaeus, 1758: 238. Type locality: Surinami (=Suriname River). Lectotype (designated here): NRM 32, 57.8 mm SL (illustrated in Linnaeus, 1754: pl. 28, fig. 4).

Hypostomus guacari Lacepède, 1803: 144, 145, pl. 4 (Fig. 2). Type locality: Les rivières de l'Amérique méridionale. Lectotype (designated here): NRM 32, 57.8 mm SL (illustrated in Linnaeus, 1754: pl. 28, fig. 4).

Loricaria flava Shaw, 1804: 38, pl. 101. Type locality: Indian Seas. Lectotype (designated here): NRM 32, 57.8 mm SL (illustrated in Linnaeus, 1754: pl. 28, fig. 4).

Plecostomus bicirrosus Gronow in Gray, 1854: 158. Type locality: in Americes Meridionalis fluminibus. Holotype or syntype: specimen illustrated in Gronovius (1754: 24, pl. 3, figs 1-2) (Ferraris, 2007: 259). Locality stated by Gronovius: "Patria ejus Surinamae Fluvius est" (=Suriname River).

Hypostomus ventromaculatus Boeseman, 1968: 65, pl. 15 (fig. 1). Type locality: Suriname River between Afobaka and Brokopondo, Suriname. Holotype: RMNH 25507. Nov. syn.

The specimen NRM 32 (Fig. 5, Tab. I, Psyn1 in morphometric analyses), 57.8 mm SL, is designated here as lectotype for *A. plecostomus*, *H. guacari* and *L. flava* to fix the identity of *Hypostomus plecostomus* and its junior synonyms, in a concern of nomenclatorial stability. The choice of the lectotype is based on literature, on the illustration of Linnaeus (1954: pl. 28, fig. 4), and on examination of the probably still only existing putative syntypes. Description of *H. plecostomus* was based on references to pre-Linnean descriptions of "*Acipenser indicus*" by Linnaeus (1754: 55) and of a "*Plecostomus*" by Gronovius (1754: 24). The specimens described by Gronovius are very likely no more in the Copenhagen's collection (Wheeler, 1989). According to Fernholm and Wheeler (1983), three specimens registered as NRM 32 may be putative type specimens of *H. plecostomus*, but very probably the smallest one is the specimen originally described by Linnaeus in 1754. The authors list several arguments in favour of this conclusion, including characteristics matching with description (small size) and illustration (absence of caudal filaments). We studied these specimens, and can confirm that the smallest one is the only one fitting with the description and illustration given by Linnaeus, leading to its designation for name-bearing type of the species. The neotype designation for *A. plecostomus* proposed by Boeseman (1968: 11) was invalid due to the existence of this name-bearing type specimen, following article 75.8 of ICZN.

The descriptions of *Hypostomus guacari* Lacepède, 1803 and *Loricaria flava* Shaw, 1804 being based on numerous literature sources including account of *Acipenser plecostomus* Linnaeus, 1758, syntypes of the latter are also syntypes of the former (Ferraris, 2007: 258). The specimen NRM 32 (57.8 mm SL) being also a syntype of the nominal species *H. guacari* and *L. flava*, its designation as lectotype for these two species as well definitely confirms their status of objective junior synonyms of *H. plecostomus*.

Figure 4. - *Hypostomus plecostomus*, Suriname, Mapana Creek, tributary of Commewijne River, MHNG 2708.047 (121.4 mm SL).

As pointed out by Fernhom and Wheeler, the two other specimens NRM 32 (81.4 and 82.0 mm SL; Fig. 6; Psyn2 and Psyn3 in morphometric analyses) are more faded than the lectotype, clearly indicating that they either did not have the same origin or not the same conditions of preservation. As it cannot be excluded that Linnaeus also examined them, they are considered possible paralectotypes. Nevertheless, as already pointed out by the morphometric analyses, their morphological characters, and in particular the numerous plates bordering the supraoccipital and the elongated caudal-fin spines (see Fig. 6) clearly show that they area not *H. plecostomus* but *H. watwata* Hancock, 1828.

Diagnosis

Hypostomus plecostomus differs from species of the *H. cochliodon* group (*H. macushi* and *H. taphorni* in the Guianas) by viliform teeth versus large spoon-shaped teeth. It differs from other Guianese species of *Hypostomus* by the teeth bearing a short roughly rounded crown, with lateral cusp about half the length of the main cusp (Fig. 7A), versus an elongated crown (Fig. 7B), with a small lateral cusp (*H. coppenamensis*, *H. corantijni*, *H. crassicauda, H. gymnorhynchus, H. nematopterus*, and *H. watwata*), or sometimes with an enlarged lateral cusp (observed in *H. gymnorhynchus* from upper Maroni River Basin only, *H. micromaculatus* and *H. paucimaculatus*). *Hypsotomus plecostomus* is also distinguished from long-crown toothed species except *H. watwata* by the presence of a preanal plate, versus absence. *H. plecostomus* further differs from *H. watwata* in having an azygous plate (sometimes divided into two to three secondary plate-

Figure 5. - *Hypostomus plecostomus*, lectotype, NRM 32, 57.8 mm SL.

lets) bordering the posterior part of the supraoccipital and directly contacting the pterotic-supracleithrum, laterally bordered by two plates that contact only the pterotic-supracleithrum (Fig. 5), versus an azygous plate (often divided anteriorly in small secondary platelets) not connecting the pterotic-supracleithrum, and with two lateral areas divided in multiple platelets (4 to 13) bordering the postero-lateral part of the supraoccipital and the posterior part of the pterotic-supracleithrum "(e.g. Fig. 6).

Description

Measurements and counts in table I. Body relatively stocky, width at cleithrum almost equal to head length (76.5-107.7, mean 97.8 ± 5.7% in HL). Dorsal profile slightly convex rising at an angle around 30° from snout tip to posterior end of supraoccipital process, then at an angle around 15° up to dorsal-fin origin, and decreasing gently from that point to end of caudal peduncle, with a slightly concave area at last dorsal-fin ray level. Ventral profile almost straight from snout tip to caudal fin. Caudal peduncle laterally compressed, elliptic in cross section. Head broad and deep (49.8-76.0, mean 63.2 ± 4.8% in HL), covered dorsally with dermal ossifications, except for small naked area at snout tip. Median longitudinal bulge associated with mesethmoid terminating

Figure 6. - *Hypostomus watwata*, possible paralectotype of *H. plecostomus*, NRM 32, 82.0 mm SL.

coequally with transversal through nares. Eye medium sized (14.2-24.2, mean 17.2 ± 2.1% of HL), dorsolaterally placed. Conspicuous ridge originating laterally to nares, passing through supraorbital, and extending to posterior portion of pterotic-supracleithrum. Supraoccipital bone with moderately to highly developed median ridge, and with relatively well developed posterior process bordered by wide predorsal plate. Predorsal region with two almost parallel ridges, area between ridges flat. Oral disk circular, its width similar to interorbital distance. Medium-sized lips, lower lip not reaching pectoral girdle, its inner surface covered with numerous small papillae. Patches of odontodes present on anterior pigmented surface of upper lip. Maxillary barbel length moderate, about one third of mouth width. Dentaries slightly curved and acutely angled, approximately 80º between left and right dentaries. Tooth sigmoid in profile, slender, with a short crown characteristic of *H. plecostomus* group, formed by short more or less rounded crown and smaller lateral cusp (external side) separated by V-shaped notch (Fig. 7A).

Sides of body covered with five rows of moderately

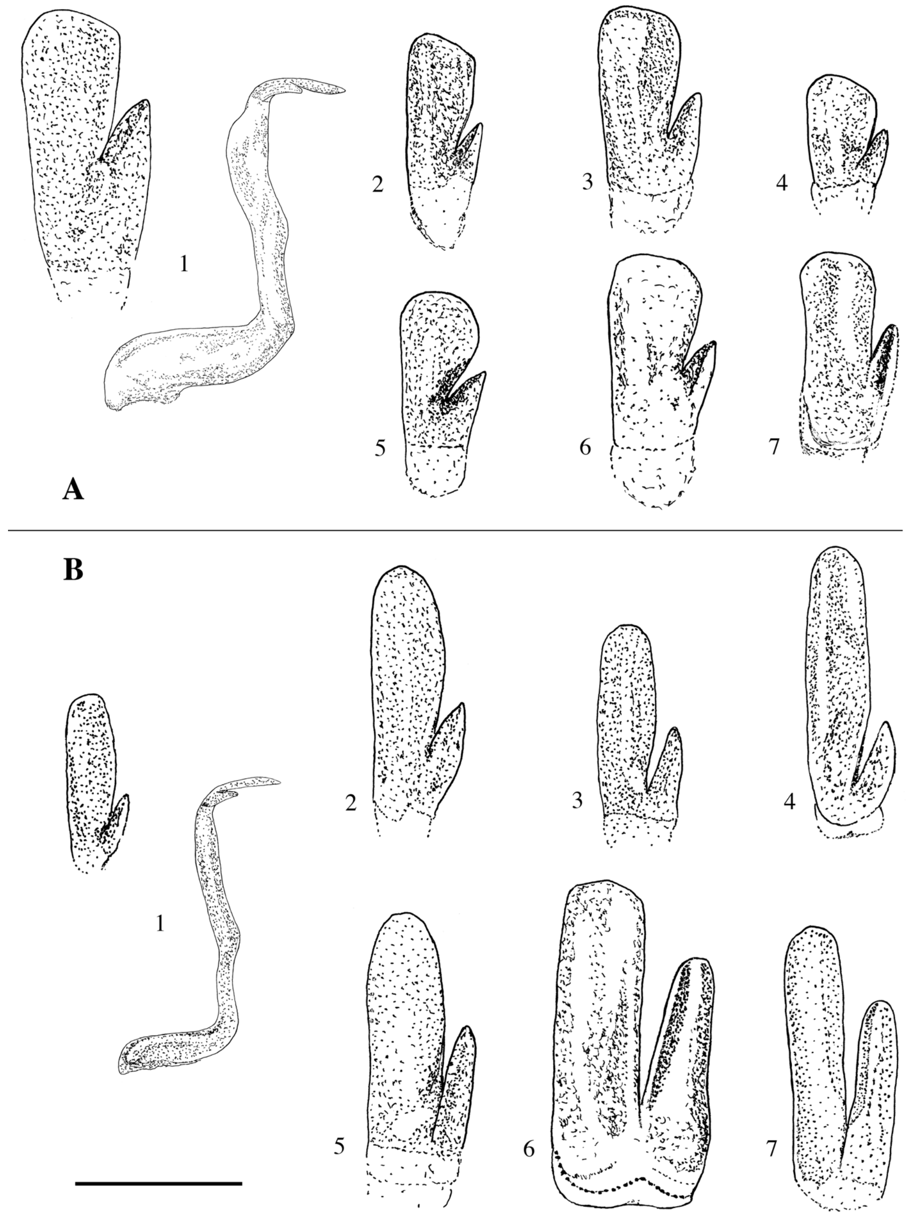

Figure 7. - Left dentary replacement teeth and tooth crowns. **A**: *Hypostomus plecostomus* from Suriname (1), Oyapock (2), Kourou (3), Commewijne (4), Suriname (5, 6), and Berbice River basins (7). **B**: Other Guinanese species of *Hypostomus*: *H. nematopterus* (1), *H. gymnorhynchus* (2), *H. crassicauda* (3), *H. corantijni* (4), *H. hemiurus* (5), *H. micromaculatus* (6), and *H. paucimaculatus* (7). Scale bar 0.2 mm for teeth and 0.1 mm for tooth crowns.

spinulose plates, all covered by small posteriorly directed odontodes. Dorsal series of plates starting at vertical through dorsal-fin spinelet and posteriorly to third predorsal plate, with weak longitudinal keel from beginning to about adipose-fin origin. Mid-dorsal series of lateral plates keeled until about end of adipose fin, forming a continued and longitudinally oriented keel on first three plates, then straight lines of elongated odontodes slightly upward oriented on each plate. Median series bearing lateral line, not keeled but bearing few larger odontodes dorsally to pores of lateral line, up to vertical of adipose fin. Mid-ventral series forming strong latero-ventral edge along first five or six plates, covered by fan-shaped lines of larger odontodes, gently decreasing in size posteriorly. Plates in ventral series not keeled along corner of ventral and lateral surfaces.

Ventral surfaces of head plated laterally, variably plated areas posterior to lower lip, cleithrum plated, abdomen covered with minute diamond shaped platelets in large specimens, except small areas around base of paired fins and urogenital opening. Single azygous plate anterior to anal-fin origin (first anal-fin pterygiophore).

Dorsal fin with anterior spinelet, laterally compressed spine, and seven branched rays. Dorsal fin large; posterior most rays reaching adipose-fin origin to adipose-fin spine, dorsal-fin margin convex. Adipose fin formed by single elevated platelet, and laterally compressed and curved spine

with membrane extending over two plates. Pectoral fin with spine, and six branched rays, first ray equal in length to spine. Pectoral-fin spine compressed and entirely covered with odontodes, aside with small fleshy extremity. Pelvic fin with one rounded spine and five branched rays; distal border straight to slightly convex. Anal fin with one flexible spine and four branched rays. Caudal fin concave, with 14 inner branched rays and elongate unbranched spine dorsally and ventrally; ventral lobe longer than dorsal lobe.

The osteology of *H. plecostomus* has been described by Schaefer (1987) based on 19 specimens from Demerara and Suriname Rivers basins, in Guyana and Suriname respectively.

Colouration

Living specimen beige-brown to brown with dark brown to blackish spots (Fig. 8A, B). In alcohol (Fig. 4), overall ground colour of body and fins brownish, lighter on ventral part. Dorsal surface of head and body entirely covered by numerous dark spots, very small and closely-set on head, larger and less closely-set along body, largest ones on caudal peduncle. Spots occasionally elongated, often coalescent, and forming more or less irregular rows along body. Angular part of lateroventral series never spotted. Pattern of colouration of ventral surface of body very variable (Fig. 10), from hardly spotted, to partly covered faded blotches and to nearly fully covered with dark spots. These spots also very variable in size and shape, and sometimes coalescent. Dorsal with rounded spots on anterior part of spine and mainly along interradial membrane, forming rows. Pectoral-fin with rounded spots, usually larger on distal part; pectoral-fin spine with small to large dark spots dorsally, and large spots ventrally. Pelvic fin with larger and wide-set spots, few paler or no spot on ventral side of spine. Rounded blotches or stripes on anal fin. Caudal fin with several vertical rows of dark spots often forming transversal stripes.

Geographic distribution

In the Guianas, *Hypostomus plecostomus* is found in the coastal region from the Oyapock River basin to the Essequibo River basin (Fig. 11). The species inhabits the lower part of rivers still under tide influence, characterized by a quiet flowing water and muddy substrate, and swamps.

Synonymy of *Hypostomus ventromaculatus* Boeseman, 1968

Two main characters were given by Boeseman (1968: 66, 33) to distinguish his new species, *H. ventromaculatus,* from *H. plecostomus*. The first one is a "deflated first dorsal fin almost or just reaching base of spine of second dorsal fin" versus "deflated first dorsal fin usually distinctly overlapping base of spine of second dorsal fin", and the second concerns ventral coloration, with "body and peduncle, including the ventral surface, covered with rather large, round, vague, dark spots" versus "body and peduncle covered with large and rather vague dark spots or blotches, lacking only on belly". This second character appeared in a key to Suriname species of *Hypostomus*, distinguishing *H. ventromaculatus* from four species including *H. plecostomus*. However examination of material shows a high variability of the ventral colouration pattern (see Fig. 10), as well as of the size of dorsal fin respective to adipose fin. For example in a single lot of 16 specimens from Lower Corantijn River (MHNG 2671.065), dorsal fin does not reach base of adipose fin in a specimen while it largely overlaps it in another, coupled with a spotted belly. In a sample from the Approuague River in French Guiana (MHNG 2713.028), previously identified as *H.* cf. *ventromaculatus*, dorsal fin almost or just reaches base of adipose fin in six specimens while it overlaps adipose-fin base in four others. These observations confirm the results of both morphological and allozyme analyses, that showed no significant difference between the populations previously identified as distinct species, and we conclude that *H. ventromaculatus* has to be considered as a junior synonym of *H. plecostomus*.

Hypostomus species in the Guianas

Based on the examination of material, on the literature, on morphometric analyses, and on allozyme electrophoresis, the validity of several species is here confirmed, some synonymies are maintained, and new synonymies are proposed. Awaiting additional work including the examination of type specimens, four species (marked below with an asterisk) still have an uncertain taxonomic status. Two of them are known only from their type specimens that are small sized and may represent juvenile forms of other described species. We nevertheless prefer to take a conservative position and include them in the following list of presumably valid species occurring from the Oyapock to the Essequibo Rivers:

- *Hypostomus plecostomus* (Linnaeus, 1758) (synonyms: *H. guacari*; *L. flava*; *H. bicirrhosus*; *H. ventromaculatus*, nov. syn.; see above)
- *Hypostomus watwata* Hancock, 1828 (synonym: *H. verres* Valenciennes in Cuvier & Valenciennes, 1840)
- *Hypostomus hemiurus* (Eigenmann, 1912)
- *Hypostomus gymnorhynchus* (Norman, 1926) (synonyms: *H. gymnorhynchus occidentalis* Boeseman, 1968, nov. syn.; *H. surinamensis* Boeseman, 1968, nov. syn.; *H. gymnorhynchus tapanahoniensis* Boeseman, 1969, nov. syn.) (*H. gymnorhynchus* species group; see below)
- *Hypostomus corantijni* Boeseman, 1968 (synonyms: *H. nickeriensis* Boeseman, 1969, nov. syn; *H. sipaliwinii* Boeseman, 1968, nov. syn.) (*H. gymnorhynchus* species group; see below)
- *Hypostomus crassicauda* Boeseman, 1968

Figure 8. - Live-color photographs of Guianese species of *Hypostomus*. **A**: *Hypostomus plecostomus* (Mapana Creek, Commenwijne River basin). **B**: *H. plecostomus* (Berbice River). **C**: *H. corantijni* (Sipliwini River). **D**: *H. crassicauda* (Sipaliwini River). **E**: *H. taphorni* (Wonotobo Falls, Corantijn River). **F**: *H. gymnorhynchus* (Crique Grillon, Orapu River). Pictures: R. Covain.

- *Hypostomus macrophthalmus* Boeseman, 1968 * (paratype: 72 mm SL, largest specimen)
- *Hypostomus micromaculatus* Boeseman, 1968
- *Hypostomus paucimaculatus* Boeseman, 1968
- *Hypostomus pseudohemiurus* Boeseman, 1968 * (holotype: 62 mm SL, largest specimen)

Figure 9. - Live-color photographs of Guianese species of *Hypostomus*. **A**: *Hypostomus hemiurus* (Kurupukari Cross, Essequibo River). **B**: *H. macushi* (Kurupukari Cross, Essequibo River). **C**: *H. micromaculatus* (Kossindo, Gran Rio River). **D**: *H. nematopterus* (Camopi, Oyapock River). **E**: *H. paucimaculatus* (Kossindo, Gran Rio River). **F**: *H. watwata* (Ouanary River, Oyapock basin). Pictures: R. Covain, except F: J.I. Montoya-Burgos.

- *Hypostomus saramaccensis* Boeseman, 1968 *
- *Hypostomus coppenamensis* Boeseman, 1969 *
- *Hypostomus nematopterus* Isbrücker and Nijssen, 1984
- *Hypostomus taphorni* (Lilyestrom, 1984)

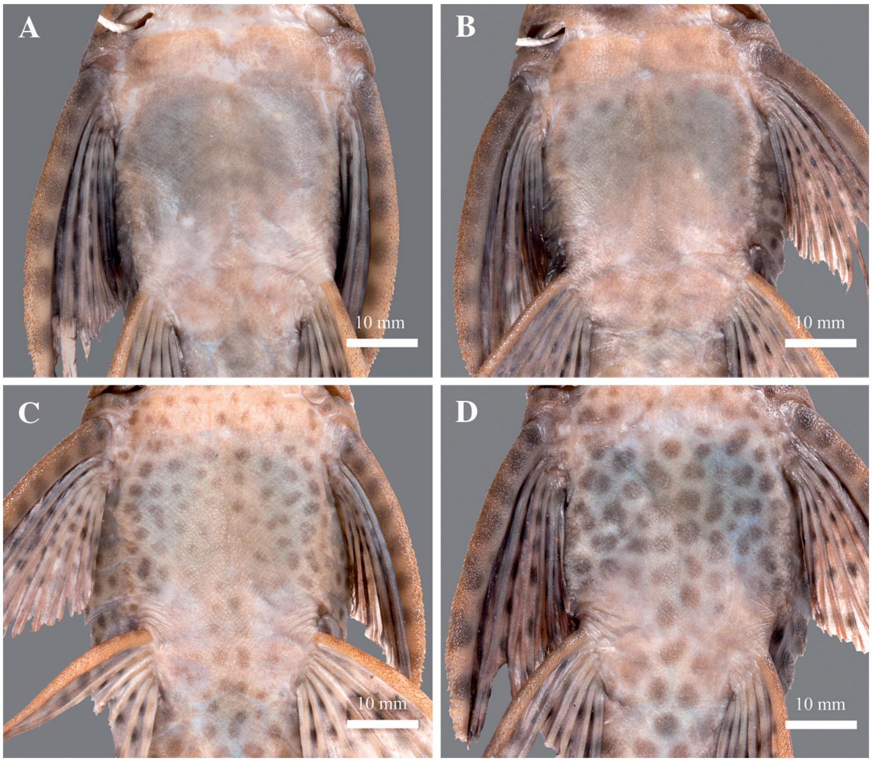

Figure 10. - Ventral colour patterns of 4 *Hypostomus plecostomus* from Suriname, Mapana Creek, tributary of Commewijne River, MHNG 2708.047.

- *Hypostomus macushi* Armbruster and de Souza, 2005

Pictures of living specimens representing all *Hypostomus* species from the Guianas but those of uncertain taxonomic status are presented in figures 8 and 9. Geographic distributions of the 15 presumably valid species, based on examined material and on literature, are indicated in figure 11.

New synonymies in the *Hypostomus gymnorhynchus* species group

Based on morphology, seven of the 15 examined nominal species of Guianese *Hypostomus* were here included in the *H. gymnorhynchus* group. The group was found very homogeneous, and clearly distinct from the other groups, however no within group difference that may distinguish any of the seven nominal species was supported by the morphometric analyses. Except *H. gymnorhynchus*, originally known from a single specimen from the Approuague River in French Guiana, all these species were originally described by Boeseman based on material originating from Suriname.

Hypostomus occidentalis and later *H. tapanahoniensis* were both tentatively described as subspecies of *H. gymnorhynchus*. They were extensively discussed (Boeseman, 1968, 1969) and placed in what Boeseman (1969: 128) named the "*gymnorhynchus*-complex". In the absence of diagnostic characters, his argumentation for these subspecies descriptions appeared nevertheless weak. As an example for describing *H. g. tapanahoniensis*, Boeseman (1969: 129) after listing arguments in favour of the presence of *H. gymnorhynchus* in Suriname, argued that "13 out of 14 species of the now known Surinam inland forms are restriced [sic] to a single river basin or (one species) to two adjacent river systems, and the identification of the single exception, the Tapanahoni *H. gymnorhynchus*, has thereby become even less acceptable". He added that "Whether these forms really represent subspecies or, more likely, good species, remains a problem only to be solved after adequate additional material becomes available." Based on our analyses of recently collected material, no difference supporting the validity of these species was found. In particular, allozyme analysis showed no allelic distinction of the population previously identified as *H. tapanahoniensis* versus the three populations of *H. gymnorhynchus*. In addition, these four *H. gymnorhynchus*-group populations showed fixed allelic differences with populations representing *H. plecostomus* and *H. watwata*, and share unique and diagnostic alleles at these loci, leading to the conclusion that this sampling represented a single valid species, namely *H. gymnorhynchus*.

Considering *Hypostomus surinamensis*, no unique character was originally given to diagnose the species which was included in Boeseman's *watwata* group (as well as all other species that form our *gymnorhynchus* group), and morphometric characters appeared very variable in this group (see Boeseman, 1969: diagrams 1 to 19). Specimens previously identified as *H. surinamensis* were here only investigated through morphology, but their data did not distinguish them from *H. gymnorhynchus*. We therefore consider the species as a junior synonym of *H. gymnorhynchus*.

H. nickeriensis and *H. sipaliwinii* are regarded as synonyms of *H. corantijni* because no unique diagnostic character was described for these species, and no evidence of a clear difference was found according to all data provided by Boeseman (see tables 2 and 11 in Boeseman, 1968, and table II in Boeseman, 1969). Moreover examination of a large number of specimens from Corantijn and Nickerie Rivers did not provide evidences for the presence of three distinct sympatric species within these basins. We thus tentatively identified specimens representing both species in our sampling based on their geographic origin and morphological congruence with original descriptions. However, morpho-

metric analyses were unable to distinguish these putative species within the group, as well as all other nominal species of the *H. gymnorhynchus* group. The single *H. corantijni* sample available for allozyme analysis was not included in present work due to insufficient electrophetic resolution, but it showed at least clearly distinctive alleles from those observed for *H. gymnorhynchus* at two loci (*Gpi-b* and *Mep-2*), and also apparently a different allelic expression at *Ldh-1* locus. These results, even when partial, sustain the validity of *H. corantijni*. A genetic delineation is thus observed between Eastern and Western Suriname.

Taxonomic status of *Hypostomus brasiliensis* (Bleeker, 1862, *in* Bleeker 1862-1863)

Hypostomus brasiliensis was since today considered a synonym of *H. plecostomus*, mainly due to the fact that a complementary description of the species by Bleeker (1864: 7) was considered to be the original description. However, Ferraris (2007: 259) rightly pointed out the correct date of availability of the name: *Plecostomus brasiliensis* was described by Bleeker in 1862 (*in* Bleeker 1862-1863: 2). This original description was solely based on the description of *Hypostomus plecostomus* Val. (not Linnaeus), and no type locality was stated. However, Valenciennes *in* Cuvier and Valenciennes (1840) explicitly based its description on “des individus de douze à quinze pouces, pris par feu M. Plée dans la lagune de Maracaïbo” (specimens of twelve to fifteen inches, collected by the late M. Plée in the Maracaïbo Lagoon), thus on specimens collected in Maracaïbo Lake in Western Venezuela. These specimens, housed in MNHN, are the syntypes of *Plecostomus brasiliensis* Bleeker, 1862. Designation of RMNH 3102, a specimen from Suriname that was used in Bleeker' complementary description, as lectotype by Boeseman (1968: 38) is therefore invalid. The taxonomic status of the species, that is not part of the Guianese fauna, has now to be revised.

DISCUSSION

Hypostomus species of the Guianas

Initially, 21 species of *Hypostomus* were recorded in fresh and brackish waters of the Guianas from the Oyapock to the Essequibo Rivers following Boeseman (1968, 1969), Le Bail *et al*. (2000), Weber (2003), Ferraris (2007), and Vari *et al*. (2009). The results of the present study sustain the validity of 15 species, of which four are regarded as doubtful and still deserve further investigations. Two additional species previously placed in *Squaliforma* Isbrücker & Michels, 2001 (*in* Isbrücker *et al*., 2001; Weber, 2003): *Squaliforma squalina* (Jardine *in* Schomburgk, 1841) and *S. tenuis* (Boeseman, 1968) are listed as *Hypostomus* by Armbruster (2004) and Vari *et al*. (2009). However, based on molecular evidences that *Squaliforma* constitutes the sister genus of *Aphanotolurus* (see Montoya-Burgos, 2003), we confirm their placement in the former. *Squaliforma* representatives are indeed known from the Magdalena, Amazon and Essequibo river basins, with *S. squalina* in Branco, Negro and Essequibo Rivers, and doubtfully from Venezuela. *Squaliforma tenuis* description was actually based on a unique specimen said to be from Paramaribo surroundings. With its elongated body and deeply forked caudal fin, inclusion of the specimen in *Squaliforma* makes no doubt, however no congeneric specimen was ever found again in Suriname despite the intense collecting effort. The type locality appears thus highly doubtful, and *Squaliforma tenuis* should better not be regarded as a Surinamese species. Two of the 15 Guianese species of *Hypostomus* belong to the *Hypostomus cochliodon* group (Armbruster, 2003), or formerly the genus *Cochliodon* Kner, 1854 which was placed in synonymy of *Hypostomus* by Weber and Montoya-Burgos (2002): *H. taphorni* (Lilyestrom, 1984) and *H. macushi* Armbruster and de Souza, 2005. These species have large spoon-shaped teeth in contrast to the viliform teeth observed in most other *Hypostomus* species including *H. plecostomus*.

Identity of *Hypostomus plecostomus* based on morphometric approach

The morphometric model used in the present study demonstrates unambiguously that the Linnean type series of *H. plecostomus* is heterogeneous and comprises two distinct species: *H. plecostomus* and *H. watwata*. The *watwata* group corresponded to different populations of the nominal species, *H. watwata*, which occurs in brackish waters along the Guianese coast. This species displayed significant morphometric structures as attested by the high statistical support observed. *Hypostomus watwata* is mostly characterized by its slender appearance with long caudal peduncle. In addition this species possesses numerous platelets just bordering the posterior portion of the supraoccipital and the pterotic-supracleithrum. This feature is perfectly visible on both possible paralectotypes of *H. plecostomus* but absent on the lectotype. The heterogeneity among the different populations of *H. plecostomus* (including those previously identified *H. ventromaculatus* and *H.* cf. *ventromaculatus*), and the lack of statistical support recorded within the *plecostomus* group made difficult the strict assignment of the lectotype of *H. plecostomus* to a given population. However, the low statistical support reflects the close morphological relatedness of all these populations. The morphometric approach remained thus insufficient to solve accurately the identity of *H. plecostomus* in regards to *H. ventromaculatus*, and complementary data were essential.

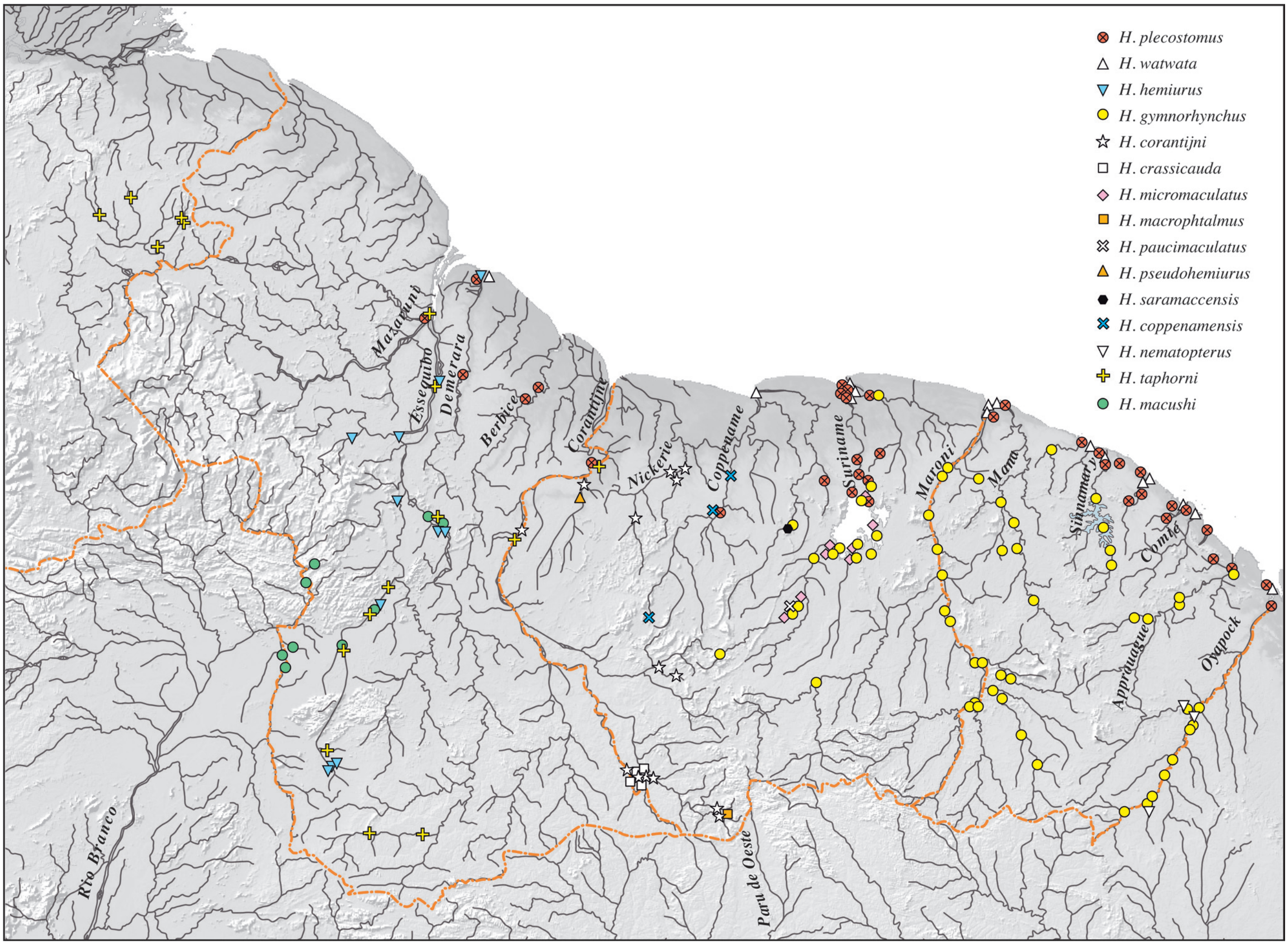

Figure 11. - Geographic distribution of *Hypostomus* species in the Guianas, based on examined material (see list) and literature (Eigenmann, 1912; Boeseman, 1968, 1969; Le Bail *et al.*, 2000; Armbruster and de Souza, 2005). One symbol may represent several localities of collection.

Genetic contribution to the delineation of species

Species limits were efficiently assessed using the allozyme electrophoresis approach. In the *Hypostomus plecostomus* group, the only significant genetic differentiations were found between the population of Kourou River and those from Oyapock and Kaw Rivers. While all three populations were initially identified as *H.* cf. *ventromaculatu*s, no difference was found between all other populations of the *H. plecostomus* group, including *H. ventromaculatus*, *H.* cf. v*entromaculatus* and *H. plecostomus*. In addition, all *H. plecostomus* group populations are distinguished from other *Hypostomus* species with fixed allelic differences, which constitute the absolute isozyme characters to distinguish species according to Davis and Nixon (1992) and Davis (1996). They were thus regarded as a single species, *Hypostomus plecostomus*, of which *H. ventromaculatus* is synonym.

Like *Hypostomus plecostomus*, *H. watwata* and *H. gymnorhynchus* were recognized based on fixed allelic differences. Genetic isolation between *H. plecostomus* and *H. watwata* is easily demonstrated as they were found in sympatry (Ouanary on the Oyapock River, Mahury River, Coswine River in Maroni basin, and Paulus Creek in Suriname basin), implying their biological species status. *Hypostomus gymnorhynchus* (and its synonym *H. tapanahoniensis*) was not found in sympatry of the two other species, but its high divergence (fixed allelic differences at four loci), in addition to morphological difference, makes no doubt about its validity. In addition to the diagnostic loci allowing unambiguous identification, each of these species was shown to have unique alleles in our sampling, in particular *H. gymnorhynchus* that showed six alleles not found in other species. With 36% of fixed allelic differences between *H. plecostomus* and *H. watwata*, 45% between *H. watwata* and *H. gymnorhynchus*, and 55% between *H. plecostomus* and *H. gymnorhynchus*, genetic divergence between these species is very high considering that populations differing at only 10% of their loci usually represent distinct species (Avise and Aquadro, 1982; Richardson *et al.*, 1986). Nei's genetic distances

values, varying from 0.558 between *H. plecostomus* and *H. watwata* to 0.933 between *H. plecostomus* and *H. gymnorhynchus*, can be compared to those reported for loricariids, that range from 0.112 up to 1.304 for other species of *Hypostomus* (de Paiva *et al.*, 2005; Zawadzki *et al.*, 2005; Renesto *et al.*, 2007), and equal to 0.51 for two species of *Ancistrus* (Fisch-Muller *et al.*, 2001) and to 0.314 for two species of *Neoplecostomus* (Zawadzki *et al.*, 2004).

Genetic diversity of *H. plecostomus*, *H. gymnorhynchus* and *H. watwata*

Hypostomus plecostomus analysed for allozymes ranged from the Oyapock River in French Guiana to the Saramacca River in Suriname. Genetic diversity between the different populations exists but it is restricted, with statistical differences found only for two cases, and with Nei's genetic distances varying from null to 0.031. Populations of Kourou and Kaw Rivers are the most divergent. They are also the most polymorphic according to P0.95 criterion (30% of polymorphic loci), and to expected heterozygosity (respectively, 0.127 and 0.109). At the species level heterozygosity (He = 0.091) is higher than the mean value indicated by Ward (1992) for fish of several orders (0.051). However, heterozygosity was indeed found very variable for numerous species of *Hypostomus* from Eastern Brazil (revised in de Paiva *et al.*, 2005; Zawadzki *et al.*, 2005; Renesto *et al.*, 2007), with values ranging from 0.000 to 0.144. It was shown that heterozygosity not only depends on population size and on taxonomic groups, but also on enzymes whose polymorphic levels diverge (Ward *et al.*, 1992; Avise, 1994). Based on the same enzyme systems studied here, values ranging from 0.040 to 0.151 were found for ten species of *Ancistrus* (Fisch-Muller, 1999), the average value (0.084) being similar to the one obtained for *H. plecostomus*.

Hypostomus gymnorhynchus also showed differentiated populations according to Nei's genetic distances, due essentially to a fixed allelic difference between Approuague and Mahury River's populations on one hand and Sinnamary and Maroni on the other; however this cannot be statistically confirmed. In addition, the four populations studied are the less polymorph of the entire *Hypostomus* sampling, two of them (Approuague and Sinnamary) showing no genetic variability at all. Such results generally indicate small population size, restricted geographical distribution and reduced gene flow between populations (Kimura and Ohta, 1971; Nei and Graur, 1984; Hamrick and Godt, 1996). On the contrary *Hypostomus watwata* is characterised by the highest genetic diversity according to all parameters examined, at both population and species levels. The high value of expected heterozygosity found in *H. watwata* (0.137) is similar to the highest value observed for *Hypostomus* and for *Ancistrus* species (see above). It clearly corresponds to species occupying a broad ecological niche (Nei and Graur, 1984; Avise, 1994), and might find an explanation in the fact that *H. watwata* is a brackish-water species able to disperse widely between lower parts of rivers through coastal waters. This result is perfectly congruent with the high morphological structure recovered within *H. watwata*.

***Hypostomus* species zonation in the Guianas**

Hypostomus representatives are found from headwaters to estuaries; however none of the species is distributed all along the course of rivers. Three main zones can be recognized according to Boujard and Rojas-Beltran (1988): the stream area of the high lands, the rivers and swamps area of coastal plain, and the estuarial and littoral area. The first zone counts the largest part of freshwaters, from headwaters to upstream of the lower falls. This biotope is mostly characterized by fast flowing waters, and a rocky substrate consisting in boulders, stones, gravels, and sand. The exposed wet rocks are also often covered by the Podostemaceae *Mourera fluviatilis* and *Apinagia richardiana*. Among other species inhabiting these rheophilic biotopes, *Hypostomus corantijni*, *H. crassicauda*, *H. gymnorhynchus*, *H. macushi*, *H. micromaculatus*, and *H. paucimaculatus* are mostly characteristic from that zone, as well as *H. nematopterus*. Known only from two type specimens collected about 40 years ago in the Oyapock River basin, the latter was regarded as a form of *H. gymnorhynchus* by Le Bail *et al.* (2000), but was later considered valid (Weber, 2003; Ferraris, 2007; Vari *et al.*, 2009). This species differs from all Guianese *Hypostomus* in having an astonishing elongation of the dorsal-fin spine, and to a less extent of the caudal-fin spines. The original illustration of the holotype shows a remarkable bony callus on the dorsal-fin spine, showing that it was once broken and had grown again, possibly longer than originally. Nevertheless, not only the paratype (examined) has the same elongated dorsal-fin spine, but also an additional specimen that we recently collected near the type locality confirms the validity of *H. nematopterus*.

The second zone comprises the areas from the lower falls to the estuary. This area is still under the tide influence and is characterized by quiet waters and a muddy substrate. Riparian vegetation often consists in the Aracea *Montrichardia arborescens*. *Hypostomus plecostomus* occupies this area.

The third zone corresponds to the estuarial and littoral area. This area is characterized by the direct influence of the sea with different levels of salinity. *Hypostomus watwata* is the only Guianese species of *Hypostomus* that is a permanent resident of this zone.

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MATERIAL EXAMINED. - Material is listed by species (present and former identifications, including new synonymies), and within each species by countries and river basins from east to west. Abbreviations for populations included in morphometric analyses are in brackets. Individual field numbers indicate specimens included in allozyme analysis.

***Hypostomus plecostomus* (Linnaeus, 1758)**

***Hypostomus* cf. *ventromaculatus* sensu Le Bail *et al.*, 2000**

Guyane française: *Oyapock River Basin* (VOya): Oyapock River, Ouanary village, close to the landing stage: MHNG 2650.049 (28 ex.), GF99-146-157, 165-172. Ouanary River: MHNG 2661.005 (6 ex); MHNG 2661.005 (5 ex). Oyapock river: MHNG 2605.056 (1 ex.). Taparabou islands: MHNG 2724.080 (1ex.). Mouth of Taparabou Creek, tributary of Oyapock River: MHNG 2724.078 (1ex.). *Approuague River Basin*: Approuague River, Régina: MHNG 2713.028 (10 ex.); Guisanbourg: MHNG 2724.081 (1ex.). *Kaw River Basin* (VKaw): Kaw River, in the vicinity of Kaw: MHNG 1223.019 (1 ex.); MHNG 1223.020 (1 ex.); MHNG 2645.012 (1 ex.), GF99-010; MHNG 2645.013 (1 ex.), GF99-014; MHNG 2645.014 (8 ex.), GF99-013, 016, 020-025; MHNG 2645.015 (1 ex.), GF99-018; MHNG 2645.016 (4 ex.), GF99-030, 032-033 ; MHNG 2713.014 (8 ex.); MHNG 2713.015 (1 ex.); MHNG 2713.016 (4 ex.); MHNG 2724.079 (1ex.); MHNG 2724.085 (2 ex.). *Mahury River Basin* (VCay): Mahury River, downstream bridge of road to Roura in front of Degrad des Cannes: MHNG 2724.076 (4 ex.), GF99-140-141, 143-144; Comté River, Saut Bief (fish farm): MHNG 2724.077 (6 ex.), GF99-071-076. Rivière des Cascades, tributary of Cayenne River: MHNG 2724.067 (3 ex.). *Kourou River Basin* (VKou): Kourou River, Soukoumou: MHNG 2595.039 (2 ex.), GF98-001, 010; MHNG 2595.042 (8 ex.), GF98-002, 006, 008-009, MHNG 2595.043 (3 ex.), GF 98-030-032. Kourou River, near Kourou: MHNG 2595.028 (2 ex); MHNG 2595.044 (1 ex), GF98-064; MHNG 2596.009 (1 ex.). Crique Couy, left bank tributary of the Kourou River: MHNG 2594.094(1 ex.). Crique des Pères: MHNG 2713.026 (1ex.). *Malmanouri Creek Basin:* Malmanoury Creek: MHNG 2713.025 (1 ex.).

***Hypostomus ventromaculatus* Boeseman, 1968**

Guyane française: *Iracoubo River Basin*: Iracoubo River, Police camp “Carbet de la Gendarmerie” MHNG 2695.069 (1 ex.); Iracoubo River, Degrad Florient; MHNG 2604.097 (10 ex.). *Maroni River Basin* (VMar): Mana River, rice fields: MHNG 2724.082. (1 ex.); MHNG 2724.083 (1 ex.); MHNG 2724.084 (2 ex.); Mana River, Awala Yalimapo: MHNG 2596.008 (1 ex.); Tupo Creek, tributary of Coswine Creek, right bank tributary of Lower Maroni River, near Ayawande: MHNG 2595.034 (2 ex.), GF98-158; MHNG 2595.036 (3ex.), GF98-151, 161; MHNG 2595.037 (2 ex.); MHNG 2595.038 (10 ex.), GF98-147, 153, 156, 163, 165-167, 170, 182; MHNG 2595.041 (2 ex.), GF98-154, 164. Suriname: *Suriname River Basin* (VSur): Paramaribo, Central Market: MHNG 2621.022 (16 ex.), SU01-010-020.

***Acipenser plecostomus* Linnaeus, 1758**

Suriname: *Suriname River Basin* (Psyn1): Surinami (=Suriname River), NRM 32 (1/3 ex, lectotype of *H. plecostomus*).

***Hypostomus plecostomus* sensu Boeseman, 1968**

Suriname: *Maroni River Basin:* Maroni River, close to James between Albina and Apatou: MHNG 2680.090 (1 ex.); Albina: MHNG 2604.019 (2 ex.). Commewijne River Basin (PMap): Mapana Creek, tributary of Commewijne River: MHNG 2708.046 (4 ex.); MHNG 2708.047 (8 ex.). *Suriname River Basin* (PPaK): Paulus Creek at mouth, right bank tributary of Lower Suriname River: MHNG 2621.023 (17 ex.), SU01- 021-037). Klass Creek, Brokopondo: MHNG 2708.042 (1ex.). *Saramacca River basin*: Mindrineti Creek, tributary of Saramacca River, near mouth of Maikaboeka Creek, Gros Rosebel Mining, MHNG 2621.032 (3ex.), SU01-046, 048-049. *Coppename River Basin*: Unnamed tributary of Coppename River near Raleigh Vallen: MHNG 2690.019 (1 ex.). Coppename River, Witagron: MHNG 2724.075 (2 ex.). *Corantijn River Basin*: Lower Corantijn River at Matapi: MHNG 2671.065 (16 ex.). Guyana: *Berbice River Basin*: Berbice River, Dubulay Ranch: MHNG 2651.066 (2 ex.). Cambo Cambo Creek, small tributary of Wuruni River, Wuruni: MHNG 2651.077 (1 ex.).

***Hypostomus hemiurus* AMNH catalogue identification**

Guyana: Essequibo River Basin (HemE): Essequibo River, Kartabo: AMNH 220361 (4 ex.).

***Hypostomus watwata* Hancock, 1828**

Guyane française: *Oyapock River Basin* (WOya): Ouanary River, tributary of Lower Oyapock River, Ouanary: MHNG 2645.009 (4 ex.), GF99-161-164. *Mahury River Basin*: Mahury River: MNHN 1903-0055; MNHN 1904-404-405. Mahury River, downstream bridge on road to Roura, in front of Degrad des Cannes: MHNG 2645.008 (1 ex.), GF99-103. *Cayenne River Basin*

(WCay): Cayenne River, Cayenne: MNHN A.8919 (1 ex.); MNHN A.9450 (1 ex.); MNHN A.9451 (1 ex.). Along sea shore beyond Pointe Macouria, Cayenne River estuary: MHNG 2650.050 (19 ex.), GF00-001-002, 004-011. *Kourou River Basin* (WKou): Kourou River, near Kourou, under bridge of RN1: MHNG 2595.029 (1 ex.), GF98-063; MHNG 2595.030 (9 ex.). *Sinnamary River Basin* (WSin): Sinnamary River, downstream Sinnamary: MHNG 2595.031 (9 ex.), GF98-098, 101, 103-104, 116-117. *Mana River Basin* (WMar): Mana River, Awala Yalimapo: MHNG 2595.024 (1 ex.), GF98-195. MHNG 2595.027 (4 ex.), GF98-184-186; MHNG 2595.033 (2 ex.). *Maroni River Basin* (WMar): Coswine Creek, near Ayawande: MHNG 2595.025 (5 ex.), GF98-146, 150, 152, 159, 162; MHNG 2595.026 (2 ex.), GF98-173, 183; MHNG 2595.032 (2 ex.), GF98-144, 155; MHNG 2595.045 (1 ex.), GF98-160; MHNG 2595.046 (1 ex.). Suriname: *Suriname River Basin* (WPuK): Pulp Creek, Paramaribo, just downstream of canal lock to Suriname River: MHNG 2621.021 (9 ex.): SU01-001-009.

***Acipenser plecostomus* Linnaeus, 1758**

Suriname: *Suriname River Basin* (Psyn2, Psyn3): Surinami (=Suriname River), NRM 32 (2/3 ex, possible paralectotypes of *H. plecostomus*).

Hypostomus hemiurus (Eigenmann, 1912)

Guyana: Essequibo River Basin: Essequibo River, Kurupukari Cross: MHNG 2651.070 (1 ex.); MHNG 2650.086 (6 ex.). Siparuni River downstream Georges Creek: MHNG 2650.084 (4 ex.). Rupununi River, Pregogo: MHNG 2651.018 (4 ex.); Dadanawa Ranch: MHNG 2651.037 (4 ex.). Arakwai River, tributary of Rupununi River: MHNG 2651.086 (2 ex.). Venezuela: *Cuiuni River Basin* (HemC): Parapapoy River, tributary of Lower Cuiuni River: UF 96192 (1 ex.).

Hypostomus gymnorhynchus (Norman, 1926)

Guyane française: *Oyapock River Basin*: Oyapock River, Saut Fourmi, upstream of Saint Georges: MHNG 2713.023 (1 ex.). *Approuague River Basin* (GApp): Crique Ipoussing: BMNH 1926.3.2.74 (holotype). Arataye River: MNHN I989-0048 (1 ex.). Arataye River, Saut Japigny: MNHN I989-0037 (1 ex.). Approuague River, rapids of Saut Mapaou: MHNG 2621.098 (9ex.), SU01-143-144, 146, 151-155, 160. *Mahury River Basin* (GCom): Crique Bagot, tributary of Comté River: 2671.005 (1 ex.). Comté River, Saut Bief: MHNG 2645.010 (7 ex.), GF99-062-068. Comté River, Lysis camp: MHNG 2671.004 (1 ex.). Crique Grillon, tributary of Orapu River, ONF camp: MHNG 2682.060 (1 ex.). *Sinnamary River Basin* (GSin): Sinnamary River, upstream Sinnamary: MHNG 2595.047 (2 ex.), GF98-091-092, MHNG 2595.048 (4 ex.), GF98-099-100,102. Sinnamary River, Saut Vata: MHNG 2724.091 (3 ex.); Saut Parasol: IRD uncat. (1 ex.). Saut Takari Tanté: MHNG 2724.092 (1 ex.). Sinnamary River, Pointe Combi: MHNG 2687.039 (1 ex.), GF98-066; MHNG 2595.035 (1 ex.). *Mana River Basin* (GMan): Mana River, Saut Fracas: MNHN 1998-1714 (9 ex.); MHNG 2724.090 (2 ex.); Saut Dalles: MHNG 2713.027 (4 ex); Saut Ananas: MHNG 2724.087. (2 ex.); Saut Capiaie: MHNG 2724.088. (2 ex.); Lezard Creek, Citron: MHNG 2724.089.

***Hypostomus tapanahoniensis* Boeseman, 1969**

Guyane française: *Maroni River Basin* (THMar): Maroni River, Saut Gostou: MHNG 2724.093 (1 ex.). Voltaire Creek, downstream Voltaire Falls, Voltaire Camp: MHNG 2683.025 (2 ex.); Voltaire Falls: MHNG 2683.040 (1 ex). Grand Inini River: MHNG 2724.096 (10 ex.); Blax Island: MHNG 2593.078 (3 ex.); MHNG 2593.080-082 (3 ex.); MNHN uncat. (2ex.); near Maripasoula: MNHN uncat. (5 ex.); Saut Lobo, Petit and Grand Inini confluence: MHNG 2724.094 (2 ex.); Saut Nicole: MHNG 2724.095 (2 ex.). Litani River, Saut Tetombé: MNHN 1998.1591 (2ex.); in the vicinity of Antecume Pata: MNHN 2000-5759 (5 ex.); 2000-5736 (2 ex.); MNHN 2000-5736 (2 ex.) ; MNHN 2000-5745 (1 ex.); MNHN 2000-5731 (1 ex.). Marouini River, in the vicinity of Antecume Pata: MNHN 2000-5778 (1ex.): MHNG 2725.001 (2 ex.); MHNG 2725.002 (2 ex.); MHNG 2725.003 (1 ex.), GF00-089; MHNG 2725.004 (3 ex.); MHNG 2725.005 (1 ex.); MHNG uncat. (5 ex.), GF00 106-108. Saut Tula Lapata: MHNG 2724.098 (1 ex.), GF00-070; MHNG 2724.099 (3 ex.), GF00-075,078-079. Aweimë Enï: MHNG 2724.100 (3 ex.), GF00-091, 093, 095. Tampoc River: MNHN 1998-1785 (9 ex.), MNHN 1998-1786 (7 ex.); Saut Kwata: MHNG 2724.097 (1ex.); Saut Pierkuru: MNHN 2000-5751 (15 ex.). Suriname: *Maroni River Basin*: Tapanahoni River: Kumaru Konde Sula: MHNG 2717.011 (9 ex.); MHNG 2717.012 (10 ex.); Tapanahoni River, Palomeu: MHNG 2717.020 (2 ex.); Palomeu River, tributary of Tapanahoni River, Wayu Camp: MHNG 2717.039 (9 ex.).

***Hypostomus surinamensis* Boeseman, 1968**

Suriname: *Suriname River Basin*: Suriname River at Jemongo: MHNG 2724.005 (1 ex.). Awaradam, rapids in Gran Rio River: MHNG 2674.009 (3 ex.). Gran Rio River, Kossindo: MHNG 2674.027 (2 ex.); MHNG 2674.044 (1 ex.). Gran Rio, Cajana Creek, left bank of Gran Rio River; MHNG 2673.045 (1 ex.); MHNG 2673.047 (6 ex.); MHNG 2673.024 (12 ex.). Gran Rio River, Assigon: MHNG 2673.077 (2 ex.).

Hypostomus corantijni Boeseman, 1968

Suriname: *Corantijn River Basin*: Oema Creek, left bank tributary of Corantijn River: MHNG 2672.022 (2 ex.).

***Hypostomus sipaliwinii* Boeseman, 1968**

Suriname: *Corantijn River Basin*: Sipaliwini River: MHNG 2708.017 (2 ex.). Sipaliwini River landing stage of Sipaliwini village: MHNG 2708.022 (3 ex.). Forest creek, Witoto Ecu, tributary of Sipaliwini River: MHNG 2708.025 (2 ex.). Sipaliwini River 15 minutes by boat downstream of Sipaliwini: MHNG 2708.034 (4 ex.). Manicouni River, upstream of mouth in Sipaliwini River: MHNG 2708.035 (3 ex.). Paikali River rapids: MHNG 2708.016 (6 ex.).

***Hypostomus nickeriensis* Boeseman, 1969**

Suriname: *Nickerie River Basin*: Nickerie River, Blanche Marie Falls West, pool at base of fall: MHNG 2621.068(3 ex.), SU01-114-116, 124, 126, 133.

***Hypostomus crassicauda* Boeseman, 1968**

Suriname: *Corantijn River Basin*: Corantijn River, Wonotobo Falls: MHNG 2672.063 (2 ex.). Sipaliwini River, Paikali River rapids: MHNG 2708.023 (12 ex.). Sipaliwini River, Sipaliwini village, landing stage: MHNG 2708.024 (4 ex.); MHNG 2708.026 (1 ex.). Sipaliwini River, rapids: MHNG 2708.033 (1 ex.), MHNG 2708.031 (1 ex.). Unnamed creek, left bank tributary of Sipaliwini River, about half an hour downstream of Sipaliwini village: MHNG 2708.037 (2 ex.).

***Hypostomus micromaculatus* Boeseman, 1968**

Suriname: *Suriname River Basin*: Gran Rio River, Kossindo: MHNG 2673.066 (1ex.), MHNG 2674.028 (1 ex.). Cajana Creek, left bank tributary of Gran Rio River: MHNG 2673.025 (2 ex.). Gran Rio River, Assigon: MHNG 2673.076 (2 ex.). Awaradam, rapids in Gran Rio River: MHNG 2674.012 (4ex.).

***Hypostomus paucimaculatus* Boeseman, 1968**

Suriname: *Suriname River Basin*: Gran Rio River, Kossindo: MHNG 2673.067 (1 ex.); MHNG 2674.043 (1 ex.).

***Hypostomus coppenamensis* Boeseman, 1969**

Suriname: *Coppename River Basin*: Coppename River, Witagron: MHNG 2604.010 (1 ex.).

***Hypostomus nematopterus* Isbrücker & Nijssen, 1984**

Guyane Française: *Oyapock River Basin*: Trois Sauts rapids of Oyapock River, 2°15' N, 52°53' W, ZMA 107804 (paratype). Oyapock River, Camopi: MHNG 2682.046 (1 ex.).

***Hypostomus taphorni* (Lilyestrom, 1984)**

Suriname: *Corantijn River Basin*: Corantijn River: Matapi: MHNG 2671.064 (7 ex.); Downstream Wonotobo Falls: MHNG 2671.075 (2 ex.); MHNG 2672.065 (1 ex.)

***Hypostomus macushi* Armbruster and de Souza, 2005**

Guyana: *Essequibo River Basin*: Essequibo River, Kurukupari Cross: MHNG 2651.073 (1 ex.). *Amazon drainage, Branco River Basin*: Sarawab River, tributary of Takutu River, Sawarab Bridge: MHNG 2651.025 (3 ex.).

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